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Ecological study of Enchytraeidae (Oligochaeta) in Norwegian coniferous forest soils

Gunnar Abrahamsen

With 24 figures

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Contents

1. Introduction

The decomposition of organic matter in nature is most probably dominated by biochemical reactions, and it is of fundamental importance for the turnover of plant nutrients, the formation of soil profiles and finally for the primary production. The decomposers of the soil consist of a variety of organisms which often are separated into primary and secondary decomposers dependant of their ability to break down the structural substances of plant material. It is a tendency to consider the primary decomposers

Contribution from the Forest Soil Fertilization Research Group, Ås-NLH (Norway).

to be most important for the decomposition. The different groups of organisms and species are, however, "working" together in an extremely complicated system which makes it very difficult to estimate the importance of the different groups or species. Therefore, it is more reasonable at the present time to presume all active and abundant groups to be of importance.

In northern coniferous forest the soil varies from highly nutritious brown earth to very poor iron podzols. In these soils the Enchytraeidae is one of the most abundant and active group of animals. Some studies on the abundance of enchytraeid worms in coniferous forest have been published (Nielsen 1955a, O'Connor 1957, Nurminen 1967a). As far as I am informed, however, no studies have been carried out on the abundance of different species in different soil types. Such information is useful in order to understand the formation of different soil types in coniferous forest, and also in the work with classification and description of soil. This is of particular interest in connection with the introduction of methods stimulating the primary production. Application of fertilizers, for example, changes the abundance and species composition of enchytraeid worms (Abrahamsen 1970) and this may be used as an indicator of more important changes in the soil conditions.

This study has therefore been carried out to examine the relation between the soil types and the abundance of the different enchytraeid species inhabiting coniferous forest soil. There is, however, a close relationship between the soil and the ground cover vegetation. Therefore, the study plots have been selected on the basis of their ground cover vegetation, and the soil and enchytraeid fauna of these plots have been described.

2. Study areas

The vegetation types were examined in three areas (A, B and C) in Southeastern Norway which is the most important forest area in this country. The specific study areas were chosen because of the adequate geographical distribution and also because different vegetation types could be found within limited areas.

The ground cover vegetation in Norwegian coniferous forest is classified into eight common vegetation types (Dahl et al. 1967). However, due to difficulties in finding good stands of all types within small areas only six vegetation types were examined at each study area (Chapter 3.2.). The position and altitudes of the study areas appear in Fig. 1.

2.1. Topography, rocks and soils

Area A is situated within the Southeastern Precambrian Area with rocks of gneiss and amfibolites. In contrast to the other areas, this area was situated below the marine limit during the last glaciation, and there is often a cover of marine sediments.

Area B is situated within the Oslo Region with permian plutonic rocks with syenite as dominating rock type.

Area C is within the Precambrian Area of Southern Norway, the so-called Kongsberg Area, with gneiss and quartzites. The sample plot on the Me-Pc ty (Chapter 3.2.) is situated on cambro-silurian shales and limestone within the Oslo Region. The rock complex in this region has undergone a slight contact metamorphism due to permian intrusives in the neighbouring Skrimfjell.

In the two areas last mentioned the soil is mainly moranic deposits, but in the floor of the valleys glacifluvial sediments also occur. The terrain in study area A is relatively flat and all sample plots have an inclination smaller than about 4°. Within the two other areas the country is hilly with variations in altitude of 400 m within a few km. The altitude of the different plots appears in Fig. 1. The inclination of some of the sample plots (Me-Pc At) of area B and C amounts to about 11°.

2.2. Climate

Climatic data have been obtained from weather and precipitation stations run by the Norwegian Meteorological Institute and the Department of Physics and Meteorology of the Agricultural College of Norway. The situation of the meteorological stations is shown in Fig. 1.

The weather station at area A is situated close to the study area. The weather stations of areas B and C, however, are situated at some distance from the study areas and also at a lower

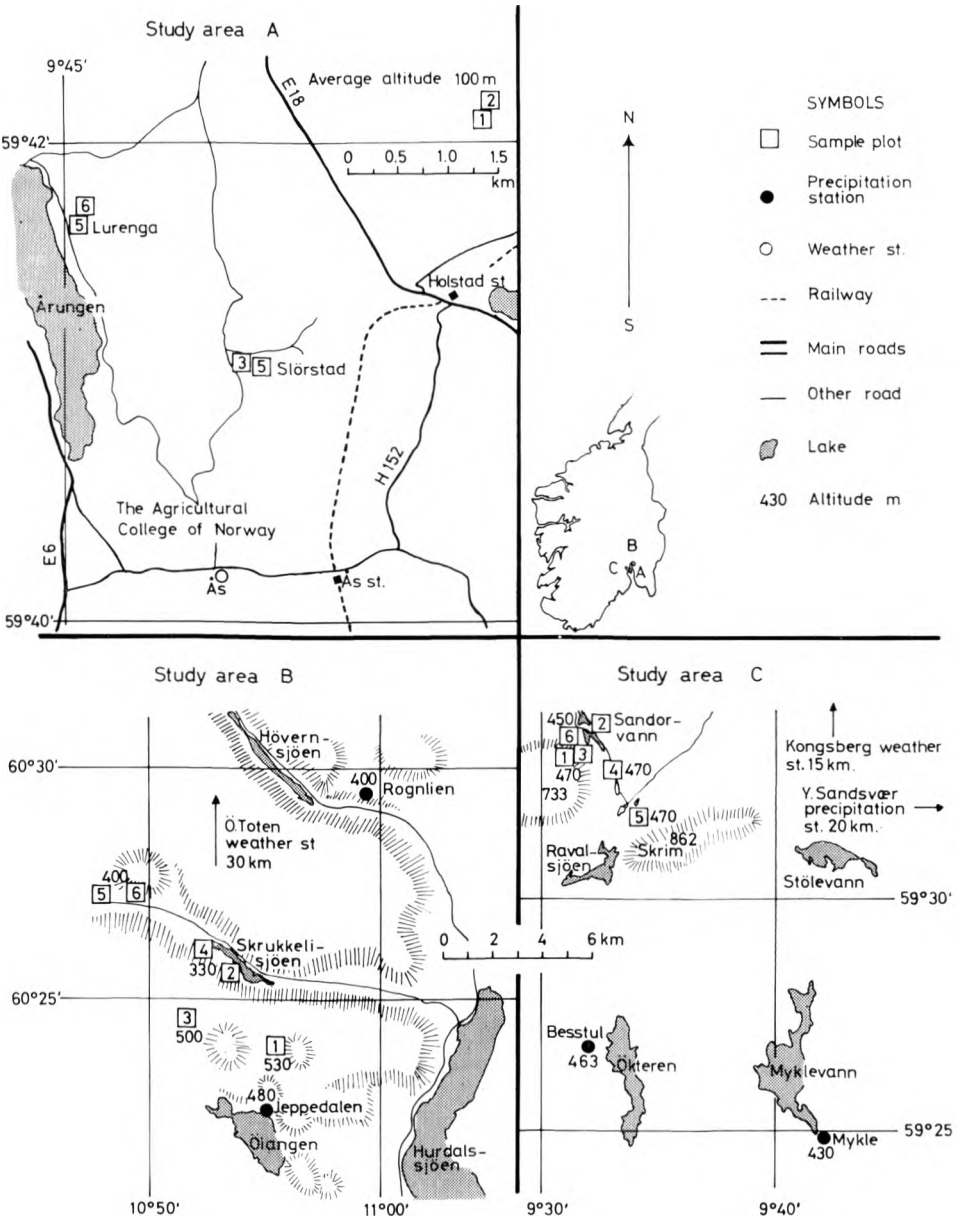

Fig. 1 The geographical position and altitude of the study areas. The number of the sample plots refers to the vegetation types: 1. **Cl-Pn** or **Ba-Pn**, 2. **Va-Pn**, 3. **Eu-Pc My**, 4. **Eu-Pc Dr**, 5. **Me-Pc ty**, and 6. **Me-Pc At** (Chapter 3.2.).

altitude (270 and 177 m respectively). In the inner parts of Southern Norway the temperature in summertime decreases on an average of 0.7 °C per 100 m increase in altitude. The average decrease in the mean temperature of the year is approximately 0.6 °C per 100 m (Det Norske Meteorologiske Institutt 1957). Approximate values of the average monthly mean temperature of sample area B and C are, therefore, obtained by subtracting 1.3 and 2.0 respectively from

the figures of Table 1. It is, however, also important to consider the variation in altitude among the sample plots within these two areas (Fig. 1).

The precipitation usually has an unknown increase with the altitude and the measurements of precipitation at Ø. Toten and Kongsberg are unsuitable to characterize the two study areas, There are, however, precipitation stations situated nearer to and at the same altitude as the study areas (Fig. 1). The precipitation at the stations within the same study area does not differ very much and, therefore, the average monthly precipitation of the stations for the years 1966, 1967, and 1968 are reproduced in Tab. 2.

Table 1 Normal air temperature (°C) in the summer half-year at the weather stations corresponding to the study areas (After Brun 1967)

Study area	Weather station	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Year
A	Ås[1])	4.3	10.2	14.4	16.8	15.6	10.9	5.7	0.9	5.5
B	Ø. Toten[1])	2.9	9.0	13.3	15.6	14.2	9.7	4.4	−0.6	4.1
C	Kongsberg[2])	4.2	10.1	14.4	16.5	15.0	10.2	4.7	−0.5	4.8

1) In the period 1931—1960; 2) in the period 1941—1960.

Table 2 Average precipitation (mm) and number of days with snow-cover for the precipitation stations corresponding to the different study areas (Det Norske Meteorologiske Institutt 1966, 1967, 1968)

Study area	Precipitation station	Jan.	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year	No. of days with snow-cover
A	Ås	37	56	45	28	84	80	63	84	77	153	94	64	866	130
B	Jeppedalen, Rognlien	62	94	59	44	101	64	72	84	105	164	117	117	1083	178[1])
C	Bestul, Mykle, Y. Sandsvaer	67	106	63	62	104	85	60	95	156	207	162	129	1297	167

1) Period 1967—1968

The reason why the averages are based on the measurements of the three years only is that the precipitation stations in area B have only been in operation since 1966. It should, however, be noted that for these years the annual average precipitation is approximately 108 and 113 % of the normal precipitation at stations in area A and C respectively.

Comparison of the temperatures and precipitation of the three study areas shows that area A is considerably warmer and drier than the two other areas. Martonne's humidity index (e. g. Hesselman 1932) for area A, B and C is 56, 77 and 88 respectively. The indices, which are based on the figures in Tabs. 1 and 2, show that area A can be characterized as humid and the two other areas as superhumid (Hesselman 1932). Area C is the most humid area examined in this study.

3. Methods

3.1. Sampling techniques

By using a certain sampling procedure, estimates with a certain degree of accuracy can be obtained. The accuracy depends both on random and systematic errors connected with the collection, storage and extraction of the soil cores. The errors connected with the storage and

extraction are dealt with in Capter 3.4. The systematic errors connected with the procedure of collecting soil cores have not been estimated. Both this and the other systematic errors are, however, common to all samples and, therefore, probably do not distort the results.

If only the random errors are considered the term accuracy which refers to the size of the deviation from the true value, should be changed to precision which refers to the deviation from the estimated value (COCHRAN 1966, p. 15). The precision of a density estimate depends on the size and number of the sample units (soil cores) and on the sampling design. However, the precision also depends on the population density and the degree of aggregation of the species. (e. g. ABRAHAMSEN 1969a). This means that in a synecological study where a standardized sampling procedure is used, the densities of the different species will be estimated with different degrees of precision.

The cylinder-shaped sampling tool used in this study has an internal diameter of 65 mm. According to a previous study (ABRAHAMSEN 1969a) this size seems to be appropriate in synecological studies. The depth of the sample units was intended to be 10 cm, but some soils, especially in areas B and C, were too stony and some of the soil cores were less than 10 cm deep. However, all sample units were deeper than 6 cm. The higher vegetation of the soil cores was cut off, but the moss layer was not removed.

The soil cores were divided into horizontal slices of 2 cm by means of a cylindrical plexiglass tool (Fig. 2). Each slice was put into individual plastic bags in the field. In addition to every second sample unit two other, equal soil cores were taken; all three as close together as possible. These which also were divided into 2 cm slices and treated individually, were used for moisture-, mechanical-, and chemical analysis of the soil. Until further treatment took place the soil cores for animal and moisture analysis were stored in a refrigator (2—3 °C), the others in a freezer.

Area A was the main study area where also seasonal variation in the fauna was studied by means of four samples taken at equal intervals during the summer half-year (Tab. 3). Relatively large sample plots were, therefore, necessary and a simple random sampling design was most appropriate (ABRAHAMSEN 1969a). Preliminary studies indicated that 20 sample units would produce estimates precise enough to discriminate among some vegetation types. Therefore, if including the sample units for moisture, mechanical and chemical analysis of the soil, 160 soil cores would be removed from each sample plot ($20\times4 + 10\times2\times4$). Due to this the sample plots were made as large as 100 sq. m. Altogether 480 soil cores were analysed for enchytraeids in area A (6×80).

In the two other study areas one sample only was to be taken from each sample plot. This meant that smaller sample plots could be used, and it was expected that a stratified random sampling would increase the precision compared with simple random sampling. The assumption for increased precision was however, that the strata got smaller than 4—6 sq. m (ABRAHAMSEN 1969a) and the strata were, therefore, made 1.75 by 1.75 m in size (3.06 sq. m). From each stratum two sample units were taken and it was assumed that 16 sample units would produce estimates with a similar precision as obtained in area A. This involved that each sample plot was 3.5 by 7 m in size and consisted of 8 strata. This size of the sample plot was considered to give representative estimates of the enchytraeid fauna (ABRAHAMSEN 1969a) as well as of the vegetation (e. g. KIELLAND-LUND 1967a). The sampling procedures are summarized in Table 3.

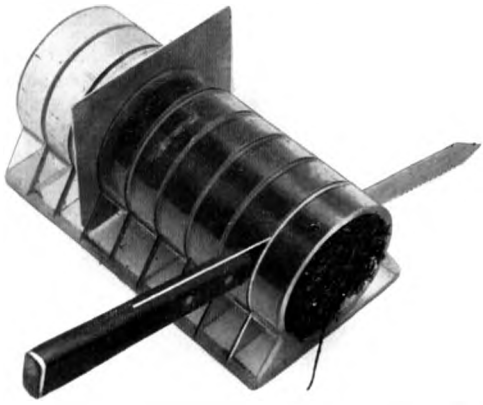

Fig. 2 The plexiglass tool used for dividing the soil cores into horizontal slices.

Table 3 The sampling procedure in the three study areas (area in sq. m)

Study area	Size of sample plots	Size of strata	No. of sample units per sample plot	Sampling date
A	100		20	22. V, 13. VII, 3. IX, 25. X 1967
B	24.5	3.06	16	11. VI 1968
C	24.5	3.06	16	28. VII 1968

3.2. Vegetation types and vegetation analysis

There is a close relationship between vegetation and soil properties in coniferous forest (e. g. Dahl et al. 1967). Therefore, the sample plots were placed on defined vegetation types comprising rich and poor soils. This vegetation system is identical to that used by Dahl et al. (1967) and it is based on investigations carried out in Southern Norway by Kielland-Lund (1962, 1965, 1967b). The system and the abbreviations used are summarized as shown below (Dahl et al. 1967).

		Studied in area
Class Vaccinio-Piceetea		
Order Cladonio-Vaccinietalia		
Alliance ?		
Association Vaccinio uliginosi-Pinetum	1. **Vu-Pn**	
Alliance Phyllodoco-Vaccinion		
Association Barbilophozio-Pinetum	2. **Ba-Pn**	B, C
Association Cladonio-Pinetum	3. **Cl-Pn**	A
Alliance Dicrano-Pinion s. str.		
Association Vaccinio-Pinetum	4. **Va-Pn**	A, B, C
Order Vaccinio-Piceetalia s. str.		
Alliance Vaccinio-Piceion		
Association Eu-Piceetum		
Myrtillus subassociation	5. **Eu-Pc My**	A, B, C
Dryopteris subassociation	6. **Eu-Pc Dr**	B, C
Association Melico-Piceetum		
Typical subassociation	7. **Me-Pc ty**	A, B, C
Athyrium subassociation	8. **Me-Pc At**	A, B, C

Partly due to differences in the climate among the sample areas the same vegetation types were not analysed in the three study areas. The **Vu-Pn** was not studied in any area also because preliminary investigations of the fauna indicated small differences among the poorest types. The **Ba-Pn** is restricted to more humid and cool regions than **Cl-Pn**. Therefore, **Cl-Pn** was studied in area A while the **Ba-Pn** was studied in the other areas.

In area A two sample plots were located on the **Me-Pc ty** and none on the **Eu-Pc Dr**. This was due to an inaccuracy in the placing of the sample plots.

The vegetation analysis was carried out by separating the plant species into tree-, shrub-, field-, and moss layer. The densities of the species were estimated by using Braun-Blanquet's cover scale which is repeated below:

(+) single specimens only; (1) 5 % cover, and few specimens only; (2) 5—25 % cover, and many specimens; (3) 25—50 % cover; (4) 50—75 % cover; (5) 75—100 % cover.

3.3. Abiotic analysis of the soil

3. 3.1. *Chemical analysis*

Ten soil cores from each sample plot in area A and 8 cores in area B and C were collected for mechanical and chemical analyses. Soil from the upper 4 cm was used for chemical analyses and soil from the 8—10 cm layer was used for mechanical studies. The chemical analyses were carried out for the first to examine relations between soil properties and the abundance of different enchytraeid species, and secondly to describe the soil of the various sample plots. For the first purpose all soil cores from three sample plots were analysed separately. Since no conspicuous relationships were found the soil cores within the other sample plots were bulked and only one series of analysis was carried out from each sample plot.

The analyses were executed at the Division of Forest Ecology at the Norwegian Forest Research Institute by standardized methods as referred to by Dahl et al. (1967).

3.3.2. *Mechanical analysis*

The mechanical analyses were also carried out by the standard methods used by the Norwegian Forest Research Institute. These analyses were performed on the mineral soil from the 8 to 10 cm layer. The soil was air dried, all visible pieces of organic material were removed and the rest was sieved through a 2 mm sieve. The fraction of mineral particles larger than 2 mm was determined. The fraction of fine sand and smaller particles was determined by the hydrometer method as used by Gandahl (1952). Particles larger than 0.074 mm were determined by sieving.

By using soil from the 8—10 cm soil layer the texture was measured in strata where the animals live. This layer, however, contained larger amounts of organic matter than the C-layer in which soil for texture analysis is recommended to be taken. The dry weight of organic matter is low and its influence on the fractions determined by sieving is of no practical importance. The results of the hydrometer method, however, may have been influenced so that the real clay content is greater than observed (e. g. Bayer 1956, p. 139). Some of the organic matter might have been removed by oxidation with hydrogen peroxide. This method has, however, several disadvantages and creates additional problems (Day 1965). Therefore, it was not used in the present study.

3.3.3. *Moisture analysis*

Soil moisture was examined to study the connection with the abundance and depth distribution of enchytraeids. It is known that the gravimetric water content (oven dried basis) is unsuitable for comparison among different soil types (e. g. Macfadyen 1963, p. 46). Measurements of the soil moisture optential (e. g. as pF), have been most used in this situation, but this was impossible to manage on the porous, root infiltrated raw humus. Therefore, an alternative method was used giving the amount of water as a fraction of the water-holding capacity at pF 0.5.

This method was carried out as follows: The individual soil slices were placed in filter bags which where closed to prevent loss of material. These were weighed immediately and submerged

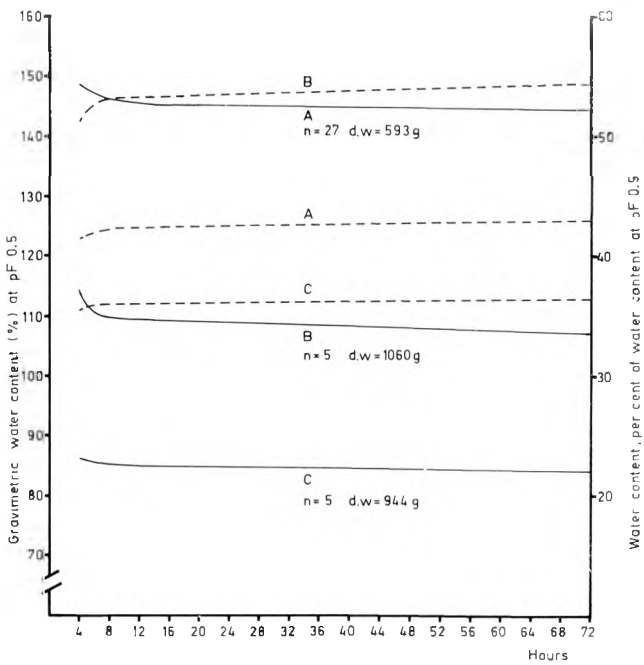

Fig. 3 The effect of increasing drainage time on the water content at pF 0.5 (over dry basis) (solid line), and on the actual water content in per cent of the water content at pF 0.5 (broken line). A = moder, B = semipodzol, C = mineral soil.

in water. To obtain maximum saturation it was necessary to keep the soil slices submerged for 5 days. Significant anaerobic activity was avoided by keeping the water cool (3 °C). The soil was then allowed to drain in air saturated with water. The effect of different drainage time appear from Fig. 3, and in this study 24 hours were used. Under the drainage period the soil slices were situated with the diameter in vertical direction. This meant that the height of the soil cores during drainage was 6.5 cm, and the average moisture tension in the soil samples was therefore, equal to 3.25 cm water or ca. pF 0.5. The water content after 24 hours drainage, which was found by weighing, drying at 105 °C and weighing again, is the water-holding capacity at pF 0.5. By adjusting for the weights of the filter bags, the natural content of water was expressed as percentage of the water-holding capacity at pF 0.5.

Compared with measurements of the gravimetric or volumetric water content, the method used is more complex and the probability of errors in the measurements is greater. Therefore, it is of interest to compare the methods. This comparison is based on soil slices from the 2—4 cm layer. It is seen that the relation between the gravimetric water content and the content in per cent of the water-holding capacity varied with the soil types (Fig. 4). The volumetric water content was, on the other hand, highly correlated with the water content in per cent of the water-holding capacity (Fig. 5). This implied that the method of giving the gravimetric water content was less suitable for the present study than the two other methods. Further, by giving the content of water in per cent of the water-holding capacity, the soil volume was not considered. This was appropriate particularly for the measurements of the upper soil slices (0—2 cm) in which the soil volume was rather variable due to different thickness of the moss layer.

3.4. Storage and extraction of soil cores

To be able to compare the vegetation types within each area with regard to the enchytraeid worms, the soil cores of the six sample plots had to be collected at approximately the same time. This involved that about 600 soil slices (in area A) were brought to the laboratory simultaneously. Due to the capacity of the extraction apparatus and the labour of the counting and identifying of the specimens some soil cores had to be stored ca. one month.

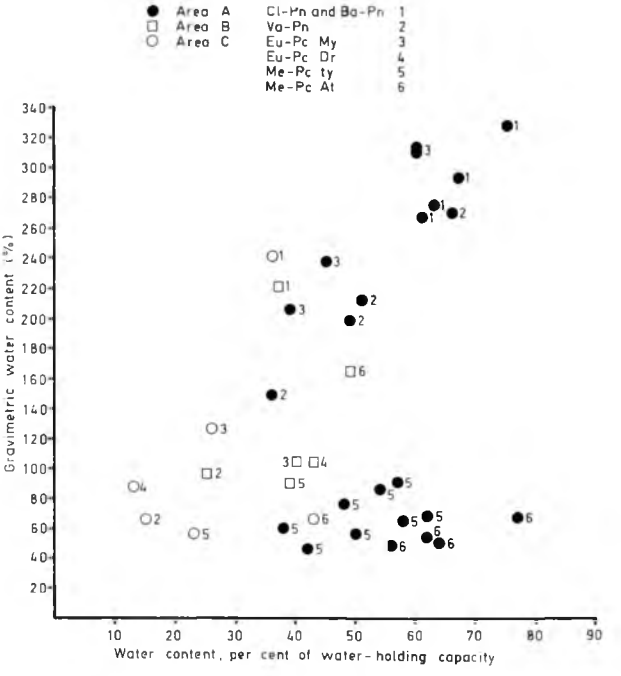

Fig. 4 Relation between the water content in per cent of the water-holding capacity at pF 0.5 and the gravimetric water content (oven dry basis).

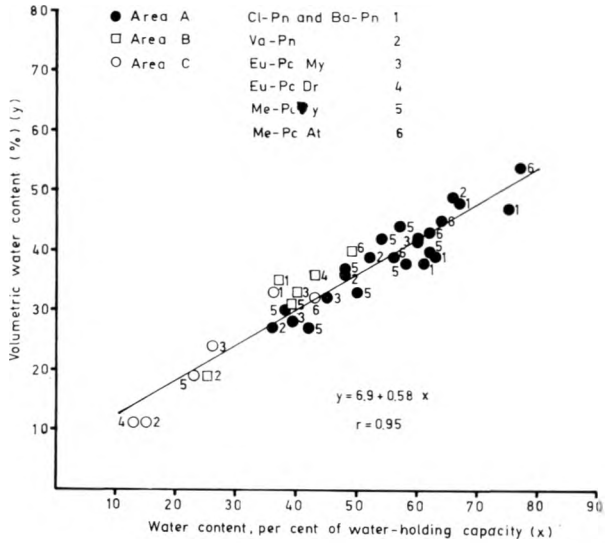

Fig. 5 Relation between the water content in per cent of the water-holding capacity at pF 0.5 and the volumetric water content.

The effect of this storage was examined by keeping soil cores in a refrigerator (2—3 °C) in different periods of time. Unfortunately this study was divided into 3 independent experiments in which different storage times were used. None of these experiments revealed significant variation on the abundance caused by the storage within a period of 3 months, but one species(*Enchytronia parva* Nielsen & Christensen 1959), was significantly ($P < 0.001$) reduced in numbers after 4 months storage.

Some periods of storage were common in the three experiments viz. 2 and 4 months. Therefore, these observations were added and the number of replicates was thus increased to 86. The mean abundance per soil core of *Cognettia sphagnetorum* (Vejdovsky 1877) for the control sample and the samples stored in two and four months were 49.9, 51.0, and 43.7 respectively. An analysis of variance revealed no significant difference among these means ($F = 1.68$, 2 and 255 df.). Hence cool storage of soil cores within one month does not seem to influence the abundance of enchytraeids in the cores.

The extraction of worms was carried out in modified Baermann funnels (O'Connor 1955). Experiments of the efficiencies of these funnels in relation to different rates of temperature increase in the soil cores were also carried out. For this purpose 150 soil cores were extracted. The temperature increase described by O'Connor (1962) was compared with a more rapid increase (50 °C in the soil surface after 2 hours) and a slower increase (38 °C in the soil surface after 3 hours). These modifications did not involve any significant differences in the number of extracted worms. In the routine use of the extraction apparatus, the heat increase was similar to that described by O'Connor (1962).

The absolute efficiency of the extraction method is almost impossible to estimate. A rough estimate may, however, be obtained by introducing a known number of worms to "sterile" soil and calculate the percentage recovery after extraction. "Sterile" soil was obtained by drying at 50 °C. Higher drying temperature made the soil unsuitable for the animals. Altogether 3.390 specimens of *C. sphagnetorum* were transferred to the "sterile" remoistened soil cores. These specimens were collected (not extracted) from cultures in homogenized humus. Extraction three days later rendered 2.938 specimens (87 %). This result is similar to the recovery percentages reported for microarthropods by Block (1966, 1967, 1970) and Brady (1969). Before and after the extraction a random sample on 192 specimens was measured alive by means of micro-photos. The mean length of these worms was 4.465 and 4.920 mm respectively, indicating that more small than large worms were lost. However, the loss of animals may be due both to the extraction and the procedure preceding the extraction. These alternatives were examined by introducing 360 specimens into petri dishes with small amounts of "sterile" homogenized humus. After three days this humus was suspended in water and carefully examined under a microscope. Of the transferred worms 84 % were recovered alive. This shows that the loss of animals observed by

extracting soil cores containing a known number of animals probably is more due to the transferring of animals to the "sterile" soil cores, than to the extraction process. The efficiency of the Baermann funnel seems, therefore, to be very high.

3.5. Counting and identification of enchytraeids

As large numbers of small and immature specimens were collected in this study, it was necessary to examine the extraction water under microscope. The identification of the species is in agreement with the descriptions given by Nielsen and Christensen (1959, 1961, 1963) and Abrahamsen (1969b).

3.6. Statistical analysis

Analysis of quantitative population data is mainly carried out by statistical methods which in theory presuppose approximate normality of the data and inequality of the variance. Numerous studies, however, have been carried out showing that some analyses, e. g. the Student's t-test and the analysis of variance, are robust against non-normality and inequality of variance (e. g. Scheffe 1959). Despite this, transformation of the data to reduce non-normality and inequality of variance has become a common procedure in density studies of animal populations. This is probably mainly due to the great non-normality of animal distributions. However, transformations do not only increase the amount of work, but the interpretation of the results is also often impeded. Therefore, in a previous study the robustness of the analysis of variance and the Student's t-test was examined by using the non-normalities found for enchytraeid counts (Abrahamsen and Strand 1970). This study in which also the effect of a transformation was examined, showed that these methods are very robust and also that the transformation is unecessary and distorting in connection with confidence intervals. In the present study, therefore, no transformation has been used.

The factors of interest to analyse in this study are the variations in abundance among vegetation types, sampling dates, and soil depths. Of interest are also interactions among these factors. The analysis of the counts was, therefore, initated by factorial analysis. The analysis is based on different models which are decisive for the test program. The model used in this study is as recommended by Ottestad (1970). However, this model presupposes a random variable and therefore, to carry out the adequate tests both sampling dates and sample plots had to be considered as random variables. Strictly speaking this was incorrect, but the incorrection is probably of small practical importance.

Variations which were found significant in the initial analysis, were studied further by means of contrast estimations. The variance of the difference between two means can be estimated by different methods. In this study the sum of the sample variances of the two means was used (e. g. Ottestad 1970). This method is a better guarantee against unexpected effects of inequalities of variances than for example the use of pooled sample variances.

4. Results

4.1. Vegetation

Table 4 gives the cover of the plant species recorded at the different sample plots. The nomenclature follows: Lid (1952), Lye (1968), Gams (1957), and Ursing (1962). The species are registered into tree-, shrub-, field-, and moss layers. Within the layers and the two orders (pine- and spruce forest) the species are tabulated after decreasing constancy.

Characteristic species of the alliance Phyllodoco-Vaccinion were *Calluna vulgaris*, *Vaccinium uliginosum*, *Orthocaulis floerkeii*, and various lichens. **Ba-Pn** was separated from **Cl-Pn** by less lichens and more *C. vulgaris* and *V. uliginosum*.

The field layer of **Va-Pn** was dominated by *Vaccinium vitis-idaea* and *V. myrtillus* and was, therefore, easily separated from the two former vegetation types. Differential species against the spruce types were lichens.

The **Eu-Pc My** was entirely dominated by *V. myrtillus* in the field layer. Differential species against the **Va-Pn** were *Luzula pilosa* and often *Sorbus aucuparia*.

Characteristic species of the **Eu-Pc Dr** were *Dryopteris phegopteris*, *D. linnaeana*, *Anemone nemorosa*, *Oxalis acetocella*.

Table 4 Synoptic table of the cover (BRAUN-BLANQUET scale) of the plant species of the vegetation types. The covers of the tree layers are give in tenths

Type:	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				Me-Pc At		
Area:	A	B	C	A	B	C	A	B	C	B	C	A_1	A_2	B	C	A	B	C
Age of forest	**110**	—	—	**110**	50	**70**	**90**	**100**	**80**	**100**	**80**	**50**	**85**	**110**	**90**	**50**	**100**	**40**
Tree layer																		
Picea abies		1					3	1	1	1	5	6	6	4	1	6	1	1
Pinus silvestris	2			3		3	1											
Alnus incana																	3	
Betula verrucosa				1														
B. pubescens					5													
Shrub layer																		
Sorbus aucuparia					+		2	1	1	1	+	1	1	2	2			2
Picea abies	+			+			+	2	+	+		+	+	+				1
Betula pubescens	+	+		+			+	+	+	+					1			1
Quercus robur				+								+	+					
Pinus silvestris	+			1														
Alnus incana																	+	
Corylus avellana																+		
Fraxinus excelsior																2		
Salix sp.					+													
Field layer																		
Vaccinium myrtillus		1	+	3	3	3	4	4	3	2	+	+	2	2	3		+	+
V. vitis-idaea	2	1	+	3	1	2	2	1	1	+	+		+	+	1		+	+
Deshampsia flexuosa	+	+		+	+		2	1	2	2	+	+	2	+	+			1
Luzula pilosa	+			+			1	+	+	1	+	+	+	+	1			+
Maianthemum bifolium					+		+	1	+	1	1	+	2	1	1	+		+
Trientalis europaea				+	+		+	+	+	+	+		1	+	+		+	+
Linnaea borealis				+	+		1	+	+	1	+		+	1	+			+
Anemone nemorosa										1	1	+	+	+	+	+	1	+
Dryopteris linnaeana								+		3	2	1	+	2	2	+		+
Oxalis acetosella										+	+	5	3	+	+	2	1	+
Sorbus aucuparia								+	+		+			+	+	+	+	
Carex digitata												1	1	+		+	1	+
Melampyrum silvaticum											+	+	+		1		+	+
Melica nutans													+	+	1	+	1	+
Viola riviniana												+	+		+	+	+	+

Table 4 (Continued)

Type:	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		De-Pc ty				Me-Pc At		
Area:	A	B	C	A	B	C	B	B	C	B	C	A_1	A_2	B	C	A	B	C
Hieracium spp.											+			+	+		+	+
Lycopodium annotinum									+	+	+	+			+			
Picea abies				+					+	+				+				+
Agrostis tenuis												+	1		+			1
Dryopteris austrica										+	1	+						
D. phegopteris										1	1					+		1
Fragaria vesca														+	+		+	+
Calamagrostis purpurea										+					+		1	
Carex pallescens															+		+	+
Filipendula ulmaria																2	2	1
Geranium silvaticum															+		1	1
Lactuca muralis														+		1		+
Milium effusum												+	+			+		
Potentilla erecta															1		+	+
Pteridium aquilinum													+			+		3
Rubus saxatilis															+		1	1
Anemone hepatica																1	+	
Deshampsia caespitosa																	1	+
Equisetum silvaticum												+						
Hypericum maculatum															+		1	
Poa nemoralis														+		+		
Ramischia secunda														+				+
Rubus idaeus												+				+		
Solidago virgaurea												+				+		
Veronica chamaedrys																	+	+
Aconitum septentrionale																	3	
Actaea spicata																+		
Alchemilla glabra																		+
Alnus incana																		+
Anthoxanthum odoratum															+			
Anthriscus silvestris												+						
Athyrium filix-femina																2		
Calamagrostis arundinacea																	1	
Carex pilulifera												1						
Chrysosplenium alternifolium																1		

Table 4 (Continued)

Type:	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				Me-Pc At		
Area:	A	B	C	A	B	C	A	B	C	B	C	A_1	A_2	B	C	A	B	C
Field layer																		
Dryopteris spinulosa												+						
Equisetum pratense																2		
Galeopsis bifida												+						
Geum rivale																+		
Impatiens nolitangere																+		
Lathyrus montanus													+					
Moneses uniflora											+							
Paris quadriflora																+		
Poa augustifolia													+					
Prunella vulgaris																		+
Ranunculus acris																		+
R. auricomus																	+	
R. repens																2		
Stachys silvatica																		
Stellaria longifolia																		
S. nemorum																2		
Trollius europaeus																+		
Urtica dioica																+		
Valerina sambucifolia																+		
Veronica officinalis														+				
Melampyrum pratense	+	+	+	+			1	+	+			+						
Calluna vulgaris	3	3	4	+														
Empetrum hermaphroditum		2	+															
Vaccinium uliginosum		2	1															
Scirpus caespitosus			+															
Moss layer																		
Pleurozium schreberi		1	2	3	1	4	3	2	3	+	1	+	2	1	2		+	+
Dicranum rugosum	2	2	+	3	2	+	+	1	+	+				+				
D. scoparium	+			+	1	1	2			+	+	+	1		1			+
Hylocomium splendens				1	+		+	2	1	2		1	1	2			1	+
Dicranum majus							2		1	1	2	+	2	+	1			1
Barbilophozia lycopodioides								1	+	1	2			+	1		+	+
Ptilium cristacastrensis							+		+	3	+	+	+	1				
Moss																		
Rhytidiadelphus squarrosus										+	1				+		1	1
Plagiochila major											+	+	1			1		+
Polytrichum formosum							1	1			+	+			+			
Brachythecium starkei												2	2			2		+

Type:	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				Me-Pc At		
Area:	A	B	C	A	B	C	A	B	C	B	C	A_1	A_2	B	C	A	B	C
Moos layre																		
Cirriphyllum piliferum																3	+	+
Mnium affine												1	1			2		
Rhodobryum roseum																+	+	+
Mnium undulatum																2		+
Rhytidiadelphus calvescens												+				2		
Thuidium tamariscinum														+			+	
Dolichotheca seligeri												+						
Plagiothecium laetum												2						
Polytrichum commune							+			+	+		+					
Sphagnum girgensohnii							+		2	1	+							
Lophocolea heterophylla							+					+			+			
Rhytidiadelphus loreus									+		+							
Plagiothecium curvifolium							+						1					
Aulacomnium palustre							+											
Cetraria islandica	+	1	+			+												
Cladonia rangiferina	2	1		+	+													
Cl. silvatica coll.	2	1	+			+												
Dicranum fuscescens		+	+			+			+									
Ptilidium ciliare	1		+	+			+											
Cladonia alpestris	2	1	+															
Polytrichum juniperinum			+	+	+													
Sphagnum nemoreum	2	2	3															
Cladonia crispata	+				+													
Cl. deformis	+			+														
Cl. gracilis			+		+													
Orthocaulis floerkii		+	1															
Webera nutans	+			+														
Cladonia chordalis				+														
Cl. coccifera spp. *Pleurota*	+																	
Cl. coniocraea	+																	
Cl. furcata				+														
Cl. gracilis f. *chordalis*	1																	
Cl. pyxidata spp. *chlorophaea*	1																	
Cl. squamosa	1																	
Cl. uncialis	1																	
Dicranum robustum			+															
D. spurium	1																	
Orthocaulis attenuatus		+																
Number of species	26	19	19	23	19	10	25	18	21	28	29	39	33	27	35	40	37	48

The best differential species of **Me-Pc ty** against the **Eu-Pe Dr** were *Melica nutans*, *Carex digitata*, *Fragaria vesca*, *Viola riviniana*, and *Melamphyrum silvaticum*.

Me-Pc At is also called the tall herb spruce forest. Conspicuous differential species against the preceding type were *Athyrium felix-femina*, *Aconitum septentrionale*, and *Filipendula ulmaria*.

The differential species mentioned were only the most important ones. Also among the mosses good differential species can be found. More detailed information on this subject is given by Dahl et al. (1967).

The differences in the species composition within the vegetation types are due to different factors. The grazing of domestic animals greatly influences the vegetation. Conspicuous grazing has occurred at the **Me-Pc At** in area B and C, and at the **Me-Pc ty** in area A (A_1). Errors connected with the registration may also have occurred. The main differences, however, were due to differences in the soil in addition to the variation in geographical and climatical conditions. The latter factors make it reasonable to consider the vegetation types to merge into one another. This "overlapping" implies that the floristic similarity (when measured by species in common) may be higher between sample plots of different vegetation types than between sample plots of the same vegetation type.

There are various indices to give the similarity between populations. The index proposed by Sørensen (1948) has probably been most used. Like other indices this one is based on the number of species (a and b) in the two localities in question and the number of species (j) in common. The index is $QS = \frac{2j}{a + b}$.

Mountford (1962) has, however, shown that QS depends on the sample size and proposed, therefore, an alternative index (I) being independent of the sample size. This index is based on the logarithmic relationship between the number of species and number of individuals (Fisher et al. 1943). By using the number of plant species QS and I were calculated for all sample plots. The results were slightly different and, as both plants- and animal communities should be treated with an analysis of similarity, the same index had to be used. However, if a (or b) equals j, $I \rightarrow \infty$ (Mountford, personal communication). I does, therefore, not discriminate between two localities if $a > b$ and $b = j$. This situation was very common in the enchytraeid data, but it is obvious that the locality having a ($> b$) species is richer than the other locality. Under these circumstances QS gives a better discrimination between the localities and mainly for this reason it has been used in the present study (Tab. 5).

Table 5 reveals that in general the similarity between sample plots within vegetation types was greater than between vegetation types. Of the 18 sample plots 11 were most similar to sample plots on the same vegetation type. The other 7 were most similar to an adjacent vegetation type within the same study area. This also appears from Fig. 6 in which the sample plots are grouped according to the procedure proposed by Sørensen (1948). The figure also shows that the highest degree of similarity was found between the plots on **Eu-Pe Dr, Eu-Pe My,** and **Ba-Pn.** The **Me-Pc At** plot in area A was most different from the others.

4.2. Abiotic analysis

4.2.1. *Soil profiles*

The soil profile was described in all sample plots. There were conspicuous differences among the vegetation types, but not among the sample areas. The plots on the *Phyllodoco-Vaccinion* were on rocky ground. The raw humus layer which was situated directly upon rocks, varied between 3 and more than 10 cm. The layer was thinner at the **Cl-Pn** than at the **Ba-Pn** (Table 6). The deepest humus layer contained peat in varying amounts

Table 5 The floristic similarity among the sample plots given by the quotient of similarity (in %)

Vegetation type	Sample area	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				M		
		A	C	B	C	B	A	C	B	A	C	B	C	B	A_2	A_1	C	B	A
Me-Pc At	A	3.0	0	3.4	0	10.2	3.2	9.8	13.8	9.2	23.2	20.6	24.0	29.9	38.4	38.0	43.2	31.2	
	B	6.4	10.7	14.3	12.8	25.0	20.0	27.6	29.1	22.6	36.4	36.9	61.1	46.9	37.2	28.9	65.9		
	C	16.2	9.0	17.9	13.8	35.8	31.0	40.6	42.4	35.5	54.5	52.6	68.7	58.7	59.3	46.0			
Me-Pc ty	A_1	10.4	17.3	15.4	12.3	27.6	29.0	40.0	42.2	46.9	53.0	50.7	48.7	42.4	63.8				
	A_2	17.0	11.5	19.2	18.6	42.3	39.3	48.2	47.1	58.7	61.3	59.0	52.9	60.0					
	B	18.9	17.4	26.1	21.6	47.8	40.0	62.5	62.3	53.8	60.8	65.5	58.1						
	C	19.7	11.1	22.2	17.8	40.7	34.5	50.0	52.8	46.7	65.7	63.5							
Eu-Pc Dr	B	25.9	17.0	29.8	26.3	46.8	58.6	73.5	69.5	64.2	80.7								
	C	18.2	12.5	20.9	20.5	41.7	34.6	63.0	59.6	59.3									
Eu-Pc My	A	35.3	27.3	21.8	34.3	54.6	62.5	69.6	65.2										
	B	31.8	27.0	43.2	28.6	64.9	58.5	76.9											
	C	29.8	30.0	45.0	32.3	60.0	54.6												
Va-Pn	A	57.2	38.1	47.7	42.4	61.9													
	B	35.6	42.2	42.2	34.5														
	C	38.9	55.2	55.2															
Ba-Pn	B	53.4	73.7																
	C	40.0																	

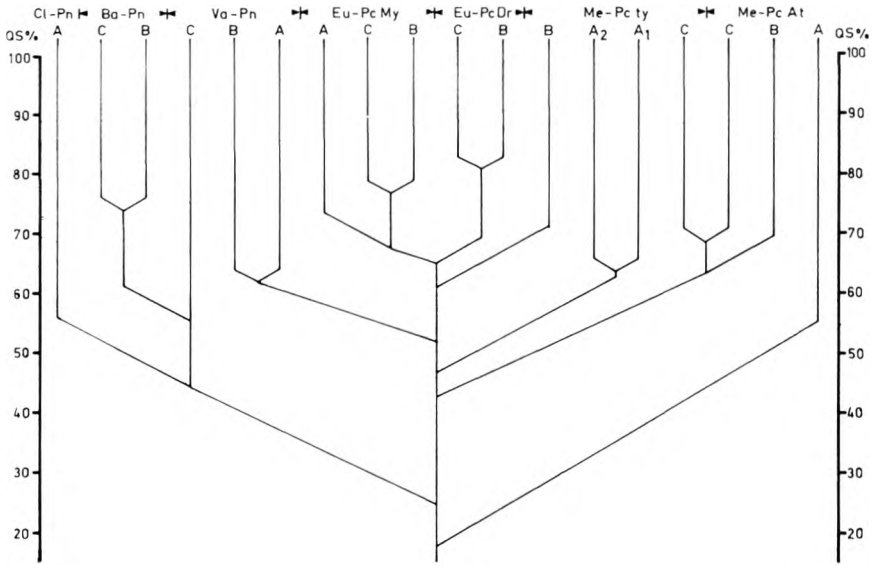

Fig. 6 Classification of the 18 sample plots by applying the quotient of similarity on the vegetation data.

both at the **Ba-Pn** and the **Cl-Pn**. The plots on **Va-Pn** and **Eu-Pc My** were found on iron podzol with thick layers of raw humus (Table 6). The Dryopteris subassociations were also on iron podzol, but the podzolization was weaker and the limits between the mineral soil and the humus (A_1 layer) were not so sharp as at the Myrtillus subassociations. The podzolization was still weaker at the **Me-Pc ty** and the profiles were classified as semipodzol and the humus as moder. At the **Me-Pc At** the mull was a moder and the profile brown earth.

Table 6 The thickness of the raw humus layers in the podzol profiles (cm)

Study area	Cl-Pn	Ba-Pn	Va-Pn	Eu-Pc My
A	ca. 7		6.4	6.8
B		8.0	5.6	7.1
C		8.0	4.7	5.2

4.2.2. *Soil texture*

The soil texture of the sample plots appears from Fig. 7. The amounts of gravel ($>$ 2 mm) are given in per cent of all fractions. In estimating the fractions of smaller particles the gravel was not included. This meant that apparently a high proportion of, for example, clay was reduced if also the amount of gravel was included. The average clay contents in per cent of particles $<$ 2 mm for area A, B, and C were 8.5, 11.4, and 4.2. If the gravel fraction was included the fraction of clay was reduced to 8.0, 8.5, and 3.1 per cent respectively. The average clay content in per cent of particles $<$ 2 mm of the soil arranged from **Va-Pn** to **Me-Pc At** were 6.7, 6.5, 5.4, 7.7, and 13.0 per cent. If the gravel fraction was included the difference in clay contents between the **Me-Pc At** and the other types was enlarged. The smaller proportion of clay at poorer sites was substituted by higher proportions of coarse sand. Conspicuous differences in the soil of the vegetation types with regard to the amounts of silt and fine sand were not observed.

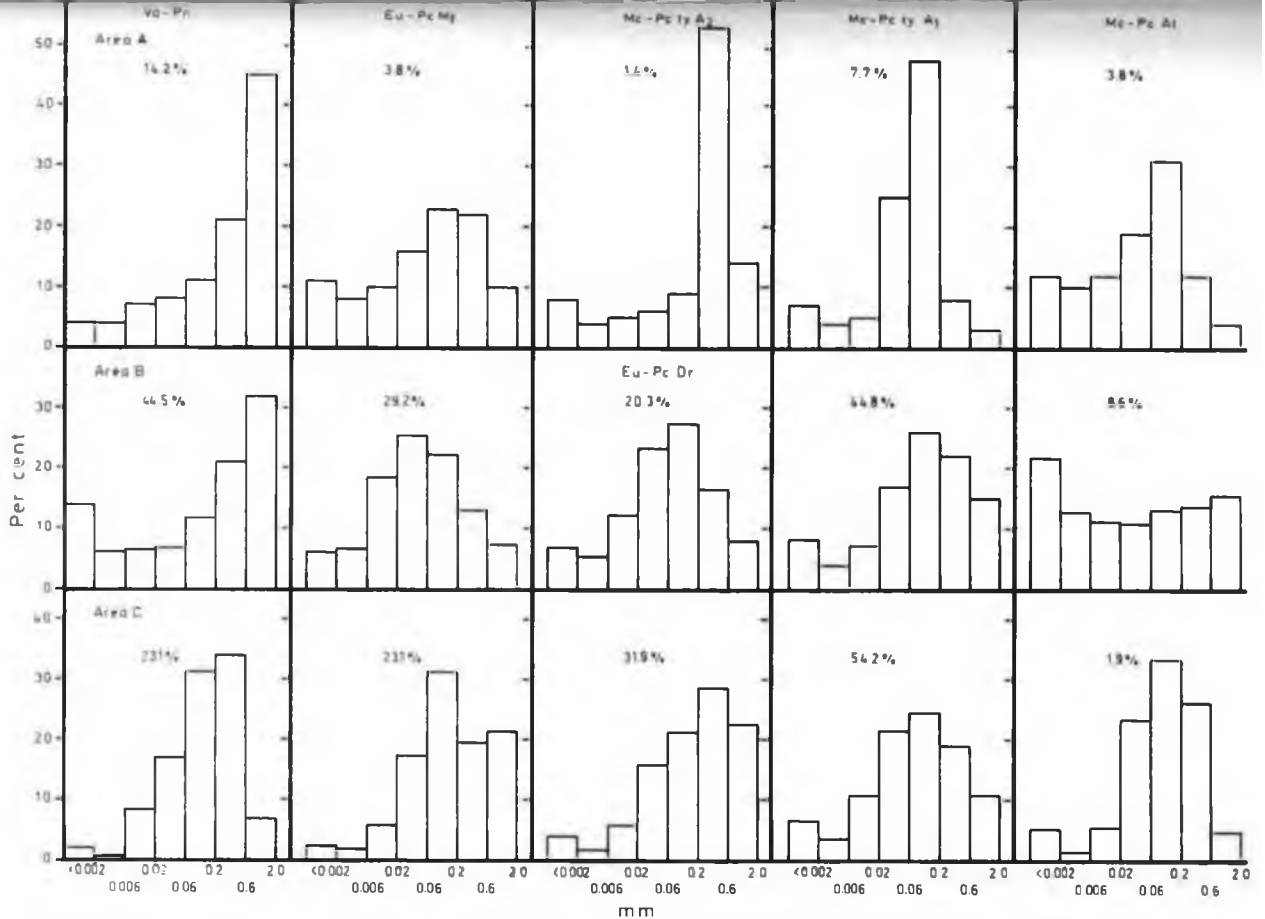

Fig. 7 Texture of the soils. Figures above the histograms give the amount of gravel in per cent of particles < 20 mm.

An exception, however, was the **Va-Pn** which was situated on soils with smaller amounts of fine particles than the other vegetation types.

Particles larger than gravel (> 20 mm) are of importance as in addition to reduce the actual life space for soil animals they also reduce the depth to which soil cores can be taken. The average depth of the soil cores may, therefore, be an approximate estimate of particles larger than about 20 mm (or the average depth of the soil above rocks; Table 7).

Table 7 The average depth (cm) of the soil cores obtained from the sample plots

Sample area	Cl-Pn	Ba-Pn	Va-Pn	Eu-Pc My	Eu-Pc Dr	Me-Pc ty	Me-Pc At
A	7.0		10.0	10.0	—	10.0 10.0	10.0
B	—	7.1	8.0	8.7	9.4	9.7	10.0
C	—	9.4	7.3	9.4	8.9	8.9	10.0

4.2.3. *Chemical properties*

The chemical analysis (Table 8) revealed that *p*H, N in per cent of loss on ignition and the base saturation in general increased from the Phyllodoco-Vaccinion to the **Me-Pc At**. Loss on ignition decreased in the same direction. The amounts of cations revealed no conspicuous trend, but the supply of Ca seemed to be greatest at the **Me-Pc At**. There were, however, also differences in the amounts of other cations, but no statistical analysis on these results was carried out as only one analysis from most of the sample plots was carried out. *p*H determinations, however, being easy to execute were performed on the individual soil cores. Statistical analysis of this material showed in general significant differences between the two **Me-Pc** subassociations, between the **Me-Pc ty** and the **Eu-Pc Dr** and also between the two **Eu-Pc** subassociations.

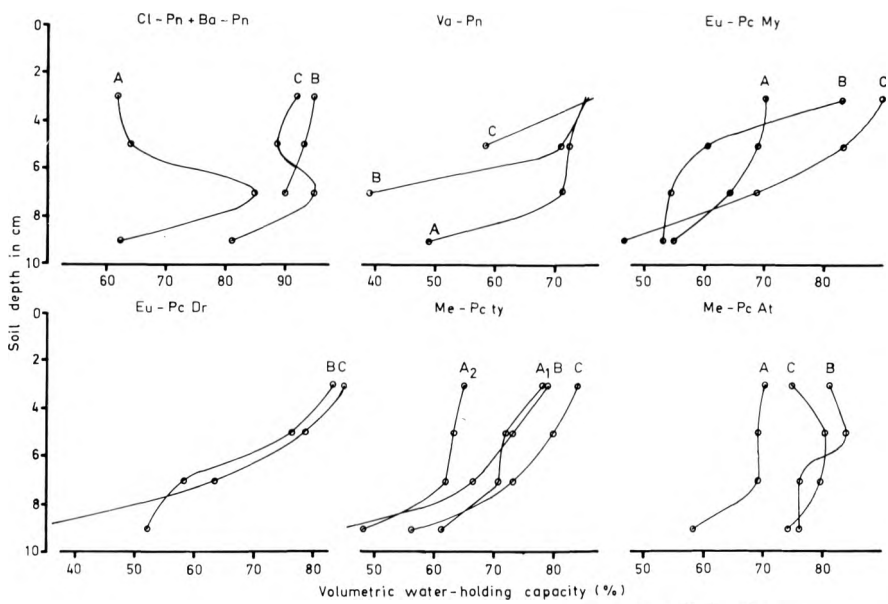

Fig. 8 The volumetric water-holding capacity at pF 0.5 in different soil depths.

Table 8 Chemical properties of the soil (0—4 cm) of the various sample plots

	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				Me-Pc At		
	A	B	C	A	B	C	A	B	C	B	C	A_1	A_2	B	C	A	B	C
*p*H	4.0	4.0	4.0	4.0	3.9	3.9	4.0	3.9	4.0	4.2	4.2	4.6	4.3	4.5	4.4	6.4	5.8	5.3
Loss on ignition %	84.0	74.0	87.1	80.8	59.1	89.6	88.5	40.5	84.5	34.0	94.3	32.0	18.2	35.5	31.8	14.4	44.7	28.3
N in % of loss on ignition	1.56	1.30	1.33	1.68	2.12	1.29	1.79	2.02	1.88	1.95	1.59	2.50	2.58	1.89	2.37	2.71	2.80	2.41
Ca me/100 g	8.2	5.6	8.3	14.2	7.0	15.1	10.4	5.1	14.5	8.5	21.6	8.9	2.3	12.1	8.1	18.3	37.8	17.6
Mg me/100 g	2.25	2.02	2.96	3.25	2.18	2.56	2.55	1.34	2.18	1.60	2.90	2.39	0.62	1.71	1.31	2.27	4.88	11.72
Mn me/100 g	0.58	0.19	0.86	1.03	0.62	0.51	0.94	0.72	1.93	0.60	1.96	0.40	0.45	0.59	0.69	0.15	0.51	0.63
Na me/100 g	0.28	0.14	0.39	0.20	0.08	0.20	0.19	0.08	0.14	0.07	0.18	0.10	0.06	0.06	0.08	0.07	0.19	0.84
K me/100 g	2.05	2.13	3.34	2.45	1.48	2.07	2.14	1.52	2.42	1.26	3.51	1.07	0.64	1.11	0.92	0.50	1.14	0.72
Cation exchange capacity me/100 g	95.4	82.9	102.5	115.3	71.9	102.7	102.5	50.0	107.5	48.1	111.4	42.2	26.2	44.1	41.2	25.8	68.5	35.2
Base saturation %	14.0	12.2	15.5	18.3	15.8	19.9	15.8	17.5	19.7	25.0	27.0	30.4	15.5	35.3	27.0	82.6	65.0	50.0

4.2.4. *Soil moisture*

Fig. 8 gives the water-holding capacity at pF 0.5 in per cent of soil volume for the different sample plots. The incomplete curves are due to inaccurate volumes in some of the layers (mosses and stones). The water-holding capacity was in general greater in the 2—4 cm layer in the raw humus than in the corresponding soil depth in the semipodzol and brown earth profiles. The decrease in water-holding capacity with increasing soil depth was, however, greater in podzols than in the other profiles. The curious variations at the **Cl-Pn** and **Ba-Pn** were due to peat layers in the soil.

Fig. 9 gives the soil moisture in per cent of the water-holding capacity. The data for the samples with the highest and the lowest water contents in area A are reproduced in the figure. The seasonal variation in the moisture in the upper 4 cm of the soil appears also from Fig. 10. The seasonal variation was reasonable when considering the precipitation in the same period (Fig. 11).

Fig. 9 also reveals that area C had the lowest water contents in the soil. Area B contained slightly more soil water. But both the amounts and the variation of the moisture content in the profiles were similar in area B and C and different from area A. These differences seem reasonable when considering the precipitation in the period before the samples were taken (Fig. 11).

4.3. Enchytraeid fauna

4.3.1. *Species composition*

The number of species increases from poor to rich soils. Tab. 9 gives the species recorded tabulated after decreasing constancy. The estimates of the densities and dominances for all species are also given. These estimates are based on the total number of individuals collected at each sample plot without correction for variation in the depth of the soil cores (Table 7). The data from area A represent the averages of the four samples.

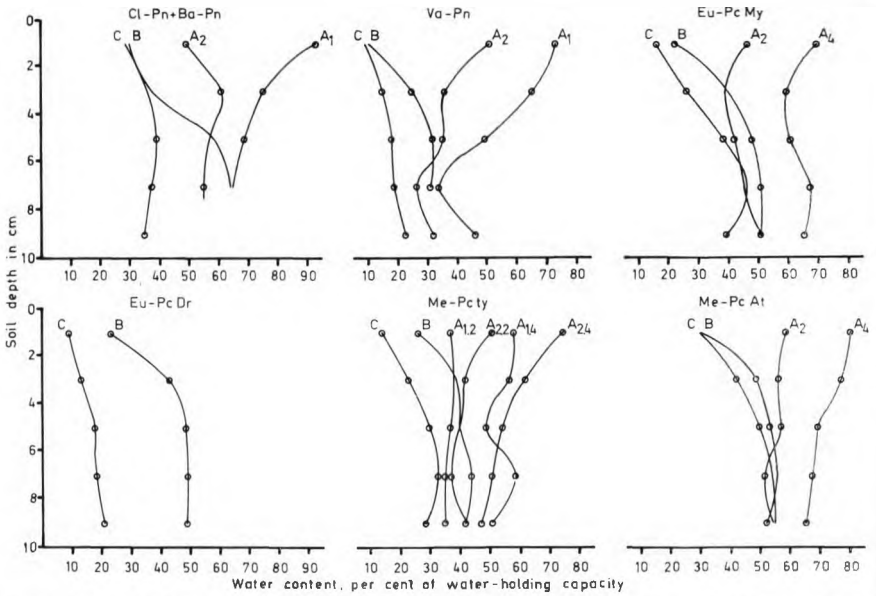

Fig. 9 Water contents in per cent of the water-holding capacity at pF 0.5 in different soil depths. The samples with the moistest and dryest soil are used from area A. The subscripts denote the sampling dates: 1 = 22. V., 2 = 13. VII., 3 = 3. IX., 4 = 22. X.

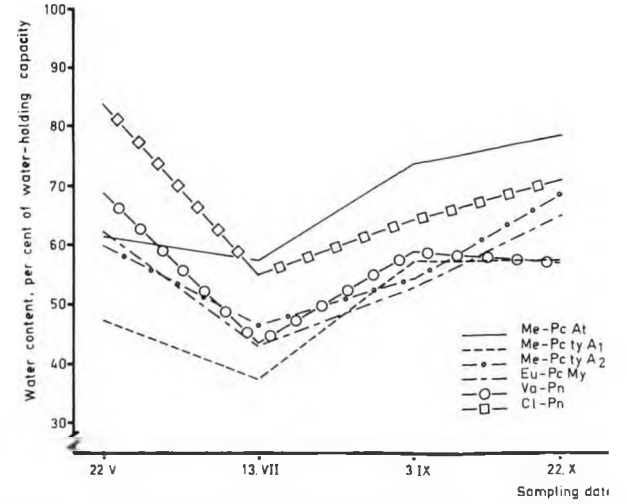

Fig. 10 The seasonal variation in the soil moisture in the 0—4 cm soil layer (area A).

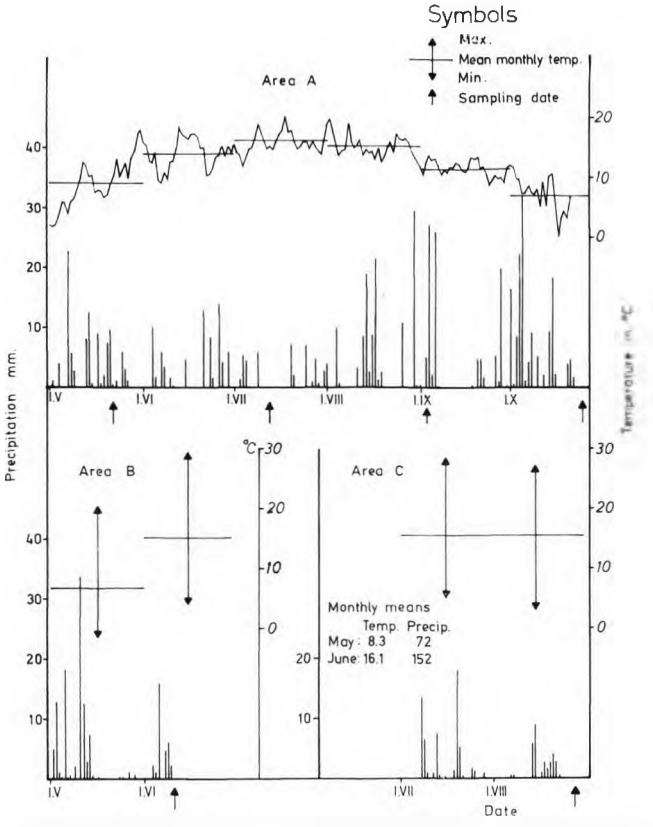

Fig. 11 Precipitation and air temperature of the study areas in the periods before sampling. The precipitation is the average of the precipitation stations. The temperatures are obtained from the weather stations and are not corrected for different altitudes.

Table 9 The densities (in thousands per sq. m) and dominances (relative abundance) of the enchytraeid species recorded. The figures from area A are the average of the four samples. Densities < 20 individuals per sq. m or dominances < one percent are marked +

		Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				Me-Pc At		
		A	B	C	A	B	C	A	B	C	B	C	A_1	A_2	B	C	A	B	C
Cognettia sphagnetorum (Vejdovsky, 1877)	No	47.0	20.2	17.3	28.1	0.94	31.2	37.2	49.9	84.2	45.4	53.5	17.5	21.3	29.6	13.3	0.35	1.10	5.2
	%	98	>99	>99	96	96	99	96	>99	>99	>99	99	44	48	83	81	1	6	10
Mesenchytraeus glandulosus (Levinsen, 1884)	No		+	0.06	0.07		0.38	+	+	0.23	0.08	0.49		0.4	0.09	1.0	0.05	0.04	0.49
	%		+	+	+		+	+	+	+		+		+	+	6	+	+	1
M. pelicensis (Issel, 1905)	No	0.77		+	0.42		+	0.13	+	+		0.24	0.04	0.22		+	+		
	%	2		+	1		+	+	+	+		+	+	+		+	+		
M. flavus (Levinsen, 1884)	No	+			0.08			0.08	0.08		0.06	0.06	0.46	0.24	0.23	+	0.08		0.08
	%	+			+			+	+		+	+	1	+	+	+	+		+
Achaeta spp.	No	0.03			0.41	0.04	+	0.75		0.09		+	3.15	1.45		0.3	0.44	0.08	0.04
	%	+			1	4	+	2		+		+	8	3		2	2	+	+
Bryodrilus ehlersi Ude, 1892	No	+			+					0.04		0.04	0.03	+	0.11				
	%	+			+					+		+	+	+	+				
Enchytronia parva Nielsen & Christensen, 1959	No				0.09			0.23			0.06		18.3	17.0	1.0	0.96	1.25	1.6	13.8
	%				+			+			+		46	38	3	6	5	8	28
Enchytraeus buchholzi Vejdovsky, 1879	No												0.04	0.12	0.26	0.47	3.55	4.6	3.05
	%												+	+	+	3	15	24	6
E. norvegicus Abrahamsen, 1969	No													3.7		0.04	+	0.08	2.75
	%													8		+	+	+	6

Cognettia glandulosa (MICHAELSEN, 1888)	No	+	+			+	0.17	0.06
	%	+	+			+	+	+
Fredericia paroniana ISSEL, 1904	No		0.31		0.26	0.02		
	%		+		2	+		
F. bisetosa (LEVINSEN, 1884)	No			0.4		+	0.21	20.3
	%			1		+	1	41
F. paroniana? ISSEL, 1904 *F. bisetosa?* (LEVINSEN, 1884)	No					0.94		
	%					4		
F. ratzeli (EISEN, 1872)	No		+			+	0.04	0.38
	%		+			+	+	+
F. galba (HOFFMEISTER, 1843)	No					1.15		80.02 8
	%					5		+
F. bulbosa (ROSA, 1887)	No					+	0.26	0.15
	%					+	1	+
F. leydigi (VEJDOVSKY, 1877)	No					0.04		
	%					+		
Marionina argentea (MICHAELSEN, 1889)	No		+			14.4	4.05	0.94
	%		+			62	21	2
Buchholzia appendiculata (BUCHHOLZ, 1862)	No					0.5	2.0	1.55
	%					2	10	3

Table 9 (Continued)

		Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				Me-Pc At		
		A	B	C	A	B	C	A	B	C	B	C	A_1	A_2	A	B	A	B	C
Hemifredericia parva Nielsen & Christensen, 1959	No																0.32	1.25	0.64
	%																1	6	1
Mesenchytraeus armatus Levinsen, 1884	No																0.26	3.65	0.3
	%																1	19	+
Henlea perpusilla Friend, 1911, augm. Cernosvitov, 1937	No																+		
	%																+		
H. nasuta (Eisen, 1878)	No																	0.11	
	%																	+	
Cernosvitoviella spp.	No																+		
	%																+		
Number of species		6	2	3	7	2	4	6	4	5	4	6	11	9	7	9	21	15	16
Total no. of individuals		47,80	20.20	17.36	29.17	0.98	31.58	33.89	49.98	84.56	45.60	54.33	39.83	44.40	31.69	16.33	23.35	19.24	49.75

Cognettia sphagnetorum was the dominating species of all sample plots except those at the Me-Pc At. Other typical species for these coniferous forest soils were *Mesenchytraeus glandulosus*, *M. pelicensis*, and *M. flavus*. The individuals of the genus *Achaeta* belong most probably to more than one species. *Achaeta aberrans* NIELSEN & CHRISTENSEN 1959, was identified, but the fraction of individuals belonging to this species was not examined. *Bryodrilus ehlersi* was very rare.

The species listed below *B. ehlersi* inhabited more nutritious spruce forest soil. *Enchytronia parva* which was a dominating species at the **Me-Pc** association, was very rare at poorer sites. *Enchytraeus buchholzi* was also typical for the **Me-Pc** association, and it was most abundant at the Athyrium subassociation. Other typical species of the **Me-Pc**, but with smaller constancies, were *Enchytraeus norvegicus*, *Fredericia paroniana*, and *F. bisetosa*. The last species was also most abundant at the Athyrium subassociation.

The best differential species between the two **Me-Pc** subassociations seemed to be *Marionina argenta*, *Buchholzia appendiculata*, *Mesenchytraeus armatus*, and *Hemifredericia parva*. Species as *Fredericia bulbosa*, *F. bisetosa*, *F. galba*, and *F. ratzeli* may also be used.

The differences in the species composition between the three richest vegetation types were quite distinct. The other vegetation types, however, were not very different with regard to the enchytraeid species. This conclusion is supported by the figures in Tab. 10 which give the quotient of similarity (SØRENSEN 1948) among the sample plots. Due to the correlation between the index and the sample size the figures from area A were based on the samples from 13. July only. The table reveals much higher degree of similarity within the **Me-Pc At** and **Me-Pc ty** than within the other vegetation types. Within the other vegetation types no systematic similarity was found. This also appears from Fig. 12 which shows the results of grouping the sample plot according to the quotient of similarity.

Two species have not previously been recorded in Norway viz. *Achaeta aberrans* and *Hemifredericia parva*. The total number of enchytraeid species reported from this country s thereby 46 (NURMINEN 1965, 1967b, ABRAHAMSEN 1968, 1969b).

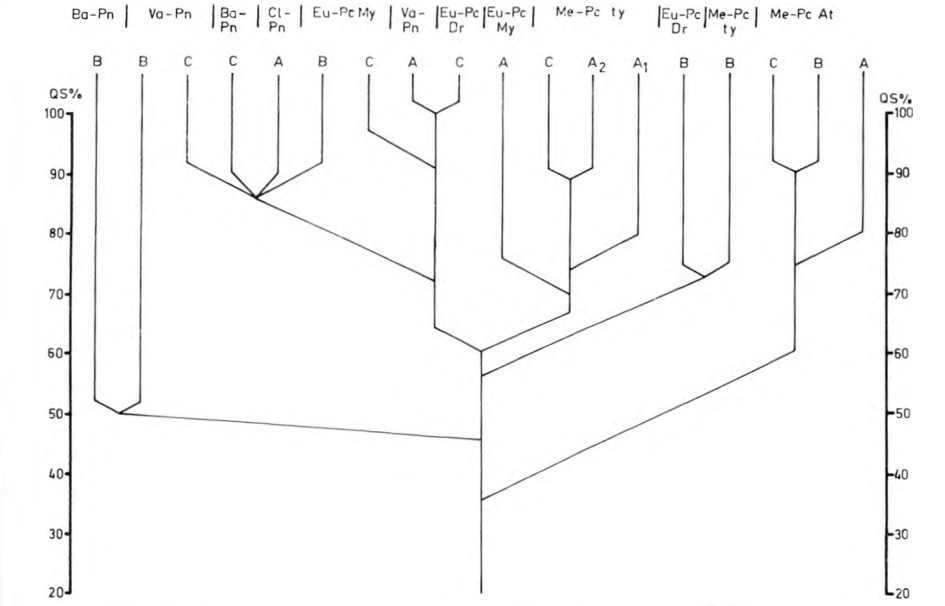

Fig. 12 Classification of the 18 sample plots by applying the quotient of similarity on the enchytraeid data.

Table 10 The faunistic similarity among the sample plots given by the quotient of similarity (in %)

Vegetation type	Sample area	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Eu-Pc Dr		Me-Pc ty				Me-Pc At		
		A	C	B	C	B	A	C	B	A	C	B	C	B	A_2	A_1	C	B	A
Me-Pc At	A	23.5	23.5	25.0	33.3	25.0	40.0	31.6	33.3	42.1	42.1	44.4	60.9	57.1	52.2	58.3	80.0	69.0	
	B	11.1	22.2	23.5	31.6	23.5	28.6	30.0	21.1	30.0	30.0	31.6	50.0	45.5	50.0	48.0	90.3		
	C	21.1	21.1	22.2	30.0	22.2	36.4	28.6	30.0	38.1	38.1	40.0	56.0	52.2	56.0	53.8			
Me-Pc ty	A_1	46.2	30.8	16.7	42.9	33.3	62.5	53.3	42.9	66.7	66.7	42.9	73.7	58.8	73.7				
	A_2	50.0	50.0	36.4	61.5	36.4	80.0	71.4	61.5	71.4	85.7	61.5	88.9	75.0					
	B	40.0	40.0	44.4	36.4	22.2	61.5	50.0	54.5	50.0	66.7	72.7	62.5						
	C	50.0	50.0	36.4	61.5	36.4	66.7	57.1	61.5	71.4	71.4	61.5							
Eu-Pc Dr	B	57.1	57.1	66.7	50.0	33.3	60.0	44.4	75.0	66.7	66.7								
	C	66.7	66.7	50.0	80.0	50.0	100	90.0	80.0	72.7									
Eu-Pc My	A	75.0	50.0	28.6	66.7	57.1	72.7	60.0	66.7										
	B	85.7	85.7	66.7	75.0	33.3	80.0	66.7											
	C	50.0	75.0	57.1	88.9	57.1	90.9												
Va-Pn	A	66.7	66.7	50.0	80.0	50.0													
	B	40.0	40.0	50.0	66.7														
	C	57.1	85.7	66.7															
Ba-Pn	B	40.0	80.0																
	C	66.7																	

4.3.2. *Abundance*

4.3.2.1. *Seasonal variation*

The seasonal variation was studied in area A. Fig. 13 gives the variation in abundance per sq. m down to 10 cm soil depht for the total number of enchytraeids and for some of the characteristic species. The figure does not reveal any systematic variation common to most species or common to all vegetation types. This conclusion was supported by the factorial analyses (Chapter 3.6.) carried out for the total number of enchytraeids, for *Cognettia sphagnetorum*, *Achaeta* spp., and *Enchytronia parva*. The analyses were carried out to examine the significance of the variations among vegetation types, soil depths, sampling dates, and interactions among these factors on the abundance of the species mentioned. However, all analyses revealed a significant interaction between the vegetation types and sampling dates. This means that significant seasonal variations have occurred, but the peak abundances at the different vegetation types did not occur at the same time.

As mentioned later (Chapter 4.3.4.) factorial analyses were also carried out for the individual vegetation types in area A to study the seasonal variation in the vertical distribution. In this way the seasonal density variation for the different species in the individual vegetation types was analysed. The results which appear from Fig. 13 reveal that the peak densities of the total number of enchytraeids and of *C. sphagnetorum* occurred in July in the pine forests and in July—October in nutritious spruce forest soil. The same difference between pine and spruce forests may also be seen with regard to the abundances of *Mesenchytraeus pelicensis* and *Achaeta* spp.

4.3.2.2. *Variation among sample plots*

The total abundance of the species in the vegetation types and sample areas appears in Table 9. In quantitative comparisons, however, equal depths of the soil cores might be used, and all figures in this chapter refer to the number down to 6 cm soil depth.

As previously mentioned the quantitative analyses of the data from area A were accompanied by factorial analyses. In area B and C, however, two-way analyses of variance were used. Those species whose densities were found to vary significantly among the vegetation types, were analysed further by means of contrast estimations. This is shown in Table 11 which gives the significance level of F in the initial analyses, the mean number of individuals per soil core, the standard deviation of the mean and the 95 per cent confidence interval of the contrasts. To make the interpretation of the table easier Fig. 14 gives the number of individuals at the different sample plots in per cent of the highest abundance recorded within each study area.

Comparisons among the study areas are of less interest but a two-way analysis of variance was carried out on the total number of individuals. This showed no significant variation among the vegetation types nor among the sample areas. This together with the results of Table 11 shows that the variation among vegetation types is not similar in the three study areas. Fig. 14 reveals that the enchytraeids were most numerous at the **Cl-Pn** in area A while the **Eu-Pc My** contained most enchytraeids in the other areas. The most numerous population comprising ca. 85.000 individuals per sq. m, was found at the **Eu-Pc My** in area C (Table 9).

The variation in the total number of specimens at poorer sites than the **Mc-Pc** association was mainly caused by *Cognettia sphagnetorum* (Table 9). At these sites the abundance of this species was almost identical to the total number of enchytraeids. Due to the significant decrease in the abundance from the **Eu-Pc** to the **Mc-Pc**, and to the **Va-Pn** the best conditions for this species seemed to be at the **Eu-Pc** and probably also at the **Cl-Pn**.

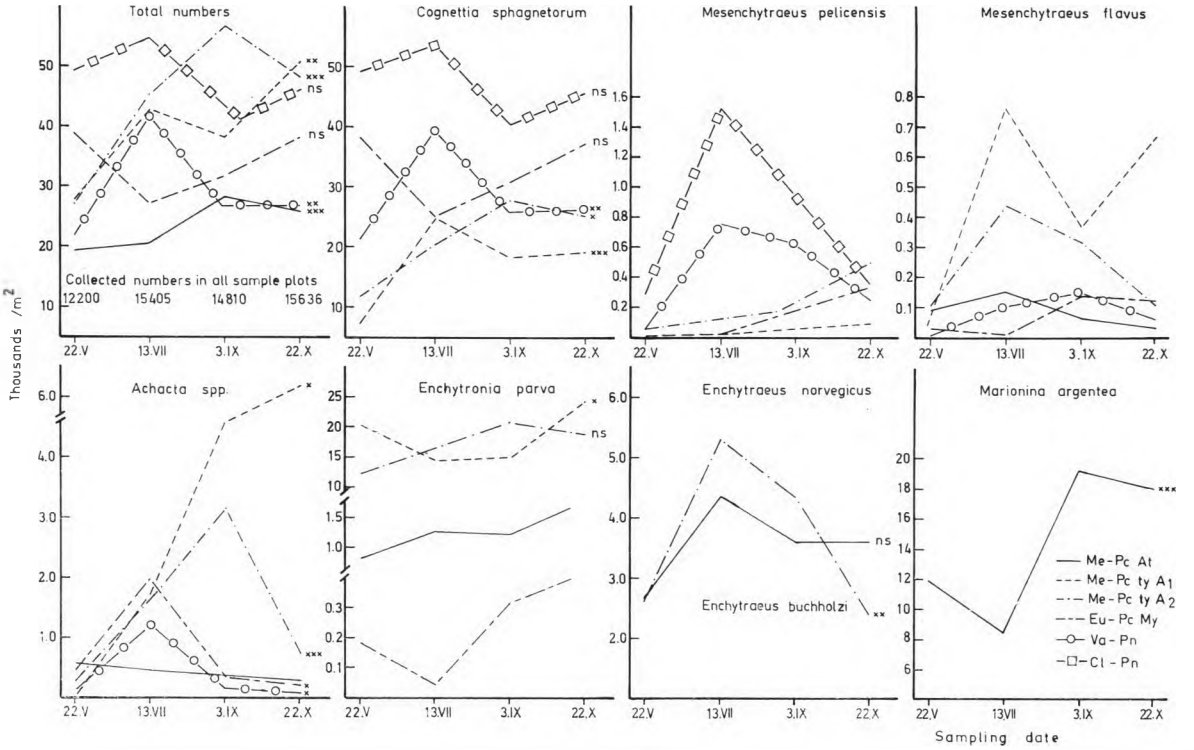

Fig. 13 Seasonal variation in the abundance of different species at the vegetation types in area A. (×) Significant at 0.05 level; (××), Significant at 0.01 level; (×××) Significant at 0.001 level; (ns) Not significant; (No symbols) Not analysed.

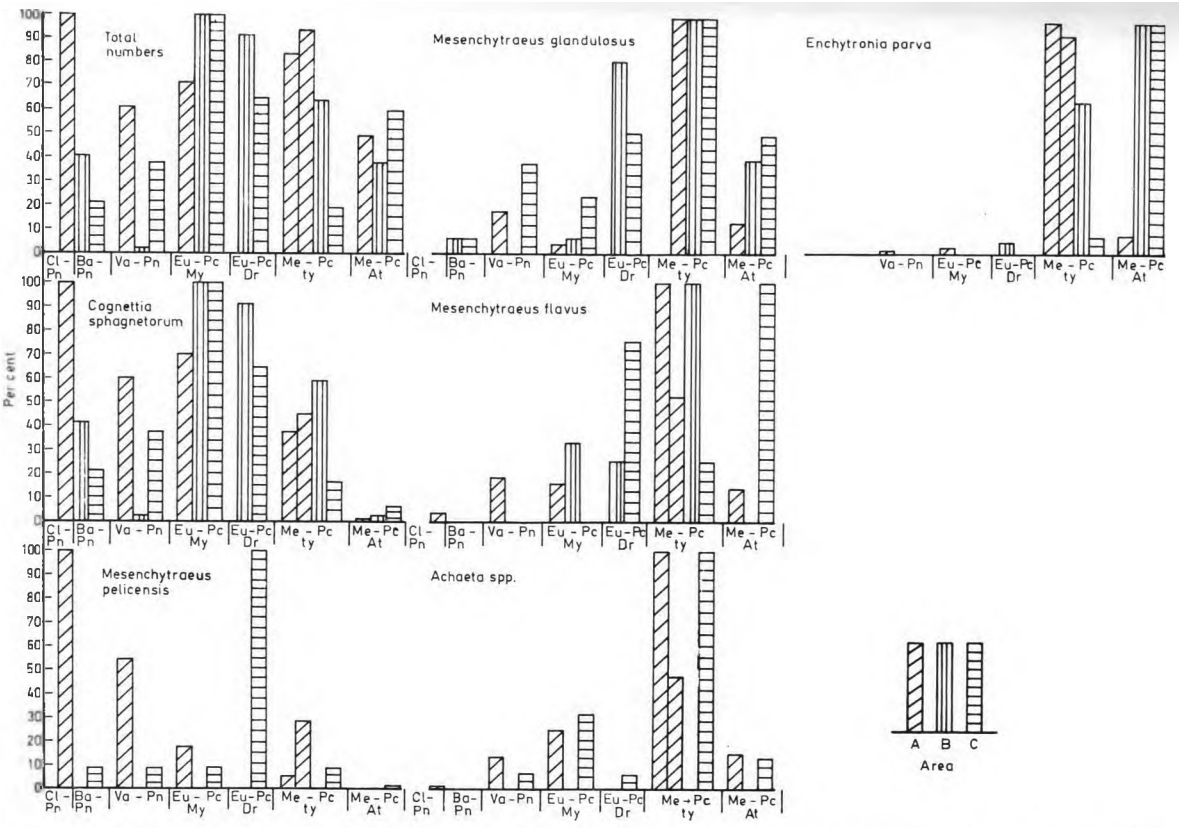

Fig. 14 Abundance of enchytraeids at the different vegetation types as percentage of the highest abundance within each study area.

Table 11 Mean number of individuals (M), the standard deviation of the mean ($S\bar{x}$) and the 95 per cent confidence intervals of the contrasts (C) given for the different enchytraeid species

Species	Study area	Sign. level of F	Mean (M) Contrast (C)	Cl-Pn	Ba-Pn	Va-Pn	Eu-Pc My	Eu-Pc Dr	Me-Pc ty	Me-Pc At
Total abundance	A	0.1 %	M	158.7 ± 13.5		96.9 ± 9.6	112.6 ± 12.5		A_1: 132.0 ± 11.9 A_2: 147.4 ± 13.5	77.7 ± 3.9
			C		**61.8 ± 32.5**	15.7 ± 30.8	A_2: 34.7 ± 36.0		$A_1 - A_2$: 15.4 ± 35.3	A_1: **54.32 ± 24.6**
	B	0.1 %	M		57.7 ± 9.5	2.63 ± 0.84	144.1 ± 16.3	109.7 ± 17.7	69.6 ± 10.3	47.1 ± 4.7
			C		**55.1 ± 19.5**	**141.5 ± 33.3**	34.4 ± 49.0		40.1 ± 41.7	22.5 ± 23.1
	C	0.1 %	M		47.6 ± 3.5	92.2 ± 21.1	245.1 ± 27.6	133.1 ± 17.2	42.2 ± 3.9	122.4 ± 27.6
			C		**44.6 ± 43.6**	**152.9 ± 70.8**	**111.9 ± 66.3**		**90.9 ± 35.9**	**80.3 ± 56.9**
Cognettia sphagneto-rum	A	0.1 %	M	156.0 ± 13.3		95.2 ± 9.1	108.6 ± 12.5		A_1: 58.0 ± 8.3 A_2: 10.5 ± 12.7	1.16 ± 0.22
			C		**60·8 ± 31.6**	13.4 ± 30.4	A_2: 28.1 ± 35.0		$A_1 - A_2$: 12.6 ± 29.8	A_1: **56.8 ± 16.2**
	B	0.1 %	M		57.6 ± 9.5	2.5 ± 0.87	143.8 ± 16.3	109.3 ± 17.7	65.0 ± 10.6	1.8 ± 0.65
			C		**55.1 ± 19.6**	**141.3 ± 33.2**	34.5 ± 49.0		**44.3 ± 42.1**	**63.2 ± 21.6**
	C	0.1 %	M		47.5 ± 3.5	91.0 ± 20.7	244.1 ± 27.4	130.4 ± 17.0	34.0 ± 3.5	12.5 ± 2.7
			C		**42.3 ± 37.7**	**153.1 ± 70.2**	**113.7 ± 66.0**		**96.4 ± 35.5**	**21.6 ± 9.0**
Mesenchy-traeus glandulosus	C	1 %	M		0.13 ± 0.09	1.13 ± 0.66	0.75 ± 0.31	1.63 ± 0.75	2.94 ± 0.46	1.38 ± 0.44
			C		1.00 ± 1.37	0.38 ± 1.49	0.88 ± 1.65		1.31 ± 1.80	**1.56 ± 1.3**
M. peli-censis	A	2.5 %	M	2.55 ± 1.00		1.39 ± 0.43	0.43 ± 0.26		A_1: 0.73 ± 0.33 A_2: 0.13 ± 0.05	0.01
			C		1.16 ± 2.13	0.97 ± 0.98	A_2: 0.30 ± 0.82		$A_1 - A_2$: 0.60 ± 0.65	A_1: **0.11 ± 0.09**
M. flavus	A	0.5 %	M	0.05 ± 0.02		0.26 ± 0.10	0.29 ± 0.07		A_1: 0.80 ± 0.28 A_2: 1.55 ± 0.39	0.28 ± 0.14
			C		**0.21 ± 0.19**	0.03 ± 0.23	A_2: 0.51 ± 0.56		$A_1 - A_2$: 0.75 ± 0.94	A_1: **1.27 ± 0.81**

Achaeta spec.	A	5 %	M	0.11 ± 0.04		1.35 ± 0.53	2.49 ± 0.59			A_1: 10.41 ± 4.16 A_2: 4.89 ± 0.99	1.48 ± 0.34
			C		**1.24 ± 1.12**	1.84 ± 1.55	A_2: **2.40 ± 2.25**	$A_1 - A_2$: 5.52 ± 8.39	A_1: **8.93 ± 8.19**		
Enchytronia parva	A	0.1 %	M			0.30 ± 019.	0.78 ± 0.37			A_1: 60.8 ± 7.5 A_2: 56.5 ± 6.6	4.13 ± 0.57
			C			0.48 ± 0.82	A_2: **55.7 ± 13.0**	$A_1 - A_2$: 4.3 ± 19.6	A_1: **56.7 ± 14.7**		
	B		M							1.50 ± 1.08	2.81 ± 0.61
			C							1.31 ± 2.53	
	C		M							2.00 ± 0.84	23.2 ± 10.5
			C							21.2 ± 21.44	

1) Me-Pc At excluded
2) Me-Pc At and Me-Pc ty excluded
3) Va-Pn excluded

Mesenchytraeus glandulosus, *M. flavus*, and *Achaeta* spp. had a similar abundance distribution on the vegetation types, and the highest population densities were found at the **Me-Pc ty** subassociation. Tab. 11 displlays significant increase in the abundance from the poorest sites and also significant decrease to the Athyrium subassociation.

The abundance of *Mesenchytraeus pelicensis* varied much among the vegetation types. In area A, however, the most abundant population was at the **Cl-Pn**.

Enchytronia parva was most abundant at the **Me-Pc** association and systematically significant differences between the two subassociations could not be found.

4.3.3. *Relation between number of species and number of individuals*

The number of species recorded in a population is a function of the number of individuals collected. Therefore, if a small number of individuals is collected the number of species in the population may be seriously underestimated. There are, however, theories considering this problem. The index of diversity (α) (Fisher et al. 1943), is a measure of the richness of species which is independent of the number of individuals collected. For large samples this theory presupposes a linear relationship between the number of species and the logarithm of the number of individuals. In Fig. 15 the cumulative number of

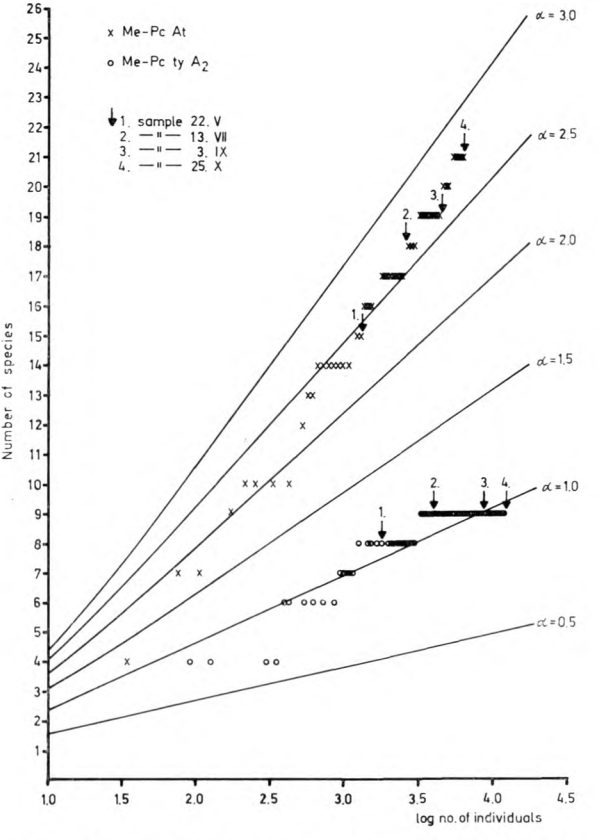

Fig. 15 Relation between the number of enchytraeid species and the cumulative number of individuals.

species at the **Me-Pc At** and the **Me-Pc ty** (A_2) in area A is plotted against the corresponding number of individuals in a logarithmic scale. It is seen that the number of species rises faster than expected according to the theory.

A feature of the logarithmic series is that the number of species represented by singletons is larger than the number of species represented by larger number of individuals. PRESTON (1948) suggested that if the number of individuals of each species was grouped into logarithmic classes (with base 2) the number of species as a function of the classes would constitute an approximate normal distribution. This means that the number of species in the first class (0—2 individuals per species) is smaller than the number of species in the second class (2—4 individuals per species). If data originated from the logarithmic series are grouped in a similar way the number of species would decrease from class I to class II. This grouping can, therefore, be used to get a rough discrimination between the two theories. WILLIAMS (1953), however, proposed to use classes separated by numbers forming a geometric progression. The first number should be 0.5 and the multiplication factor could be any odd number.

This procedure with a $\times$ 5 classification has been applied to the enchytraeid counts of the richest sample plots (Fig. 16). If data from the logarithmic series are treated in

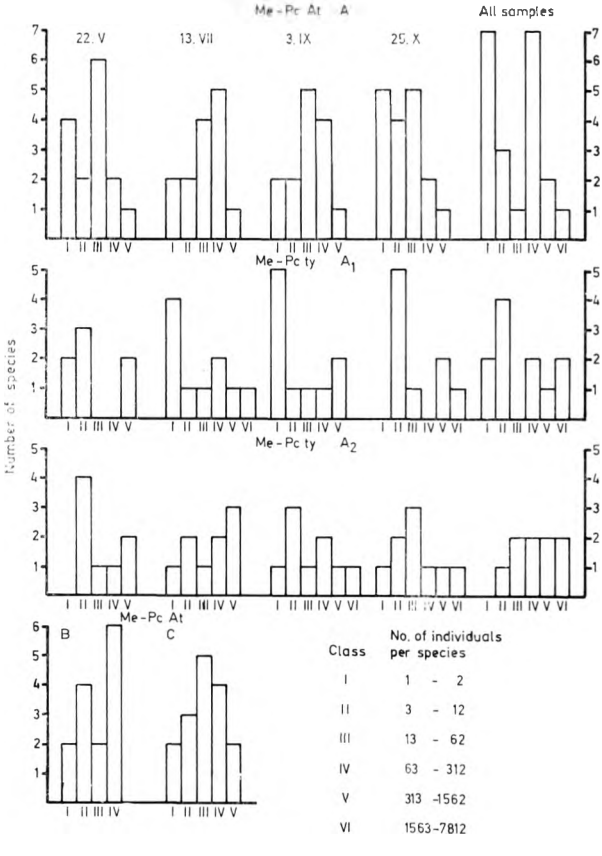

Fig. 16 Frequency distribution of enchytraeid species represented with different number of individuals, grouped in a $\times 5$ geometric classification.

this way, the number of species in class I in per cent of some of the other classes depends on the sample size (x-value), but the number of species in the peak classes cannot be larger than ca. 107 % of the number of species in class I. Fig. 16 shows that the number of species in class I in general is too small to fit the logarithmic series (the x-value is larger than 0.99 in all counts). The conclusion, therefore, is that the enchytraeid counts seem to be better fitted by the log-normal distribution than by the logarithmic series.

As the logarithmic series implies a linear relationship between the number of species and the log-number of individuals, the number of species has no limit as long as the number of individuals increases. The log -normal distribution on the other hand implies a sigmoid relationship between the number of species and log-number of individuals. This means that the number of species in any population is finite. This number can be estimated by means of the technique proposed by GRUNDY (1951). This calculation showed for the enchytraeid data that in average 89 % of the species have been found and the number of unrecorded species varies according to this from zero to two.

The estimates of the total number of species in the population imply that the "minimal area" or the minimal number of individuals or sample units, necessary to obtain a certain fraction of the species in the populations can be estimated. In Fig. 17 species-individual curves are shown for different sample plots. The number of species is expressed as percentage of the estimate of the total number of species in the population. The figure also shows examples of the number of sample units corresponding to the number of individuals. If the number of sample units was used at the abscissa the variation among the curves would have increased. It can be noticed that the number of individuals necessary to obtain e. g. 80 % of the species may sometimes be as large as ca 4500. It is also seen that the "minimal number of individuals" seems to vary as much within a vegetation type as among the vegetation types.

The departure from the logarithmic series is hardly great enough to invalidate the use of α to describe the fauna. Therefore, in Table 12, α is given for the different sample

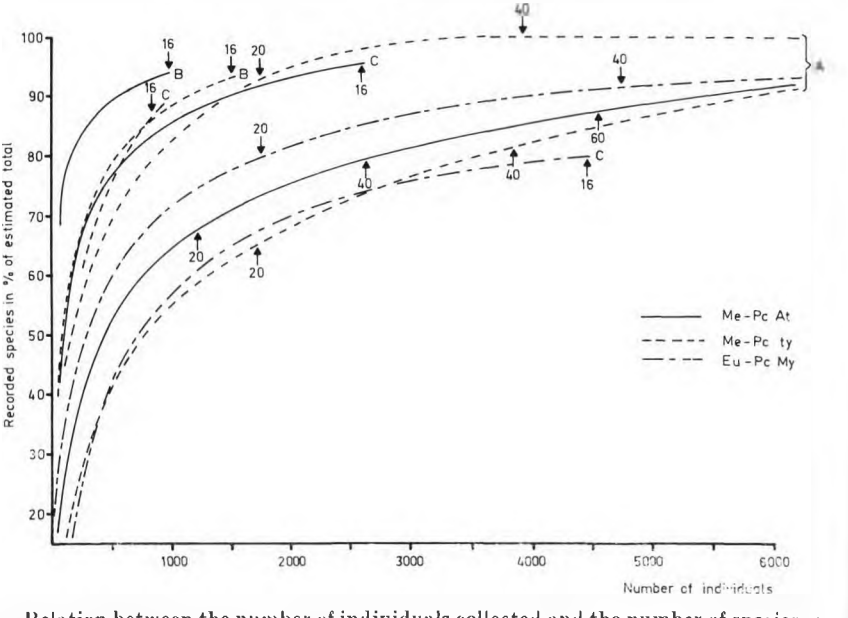

Fig. 17 Relation between the number of individuals collected and the number of species recorded in per cent of the estimates of the total number of species.

plots together with its standard deviation and the 95% confidence intervals of the contrasts within the sample areas. The figures from area A are based on the average number of species and individuals in the four samples. Significant contrasts are only found among the richest spruce forest types and between the two pine forest types in area A. With exception of the **Va-Pn** the indices within the vegetation types (among the study areas) are hardly significantly different. However, the diversity of the fauna in area B seems to be less than in the other areas.

4.3.4. *Vertical distribution*

Differences in vertical distributions are usually analysed by means of the χ^2 method. In the present study it was of interest to compare the vertical distribution of the different species at different sampling dates and soil types. This would demand a large number of analyses of which a certain proportion (e. g. 5%) had to give significant differences due to random variation. This problem can be reduced by reducing the number of analyses. Therefore, the factorial analysis is to be preferred. By this method the variations in the vertical distribution among sampling dates and sample plots were tested by means of the interactions in the abundances among soil layers on the one hand, and the sampling dates and sample plots on the other hand.

However, both the latter analysis and the χ^2 were based on the total number of individuals in the different layers. The random variation within the samples (i. e. between the soil cores) could not be considered. When concerning the data in area A this variation could be included by using separate factorial analysis (complete randomization) of each sample plot (Chapter 4.3.2.1.). The number of significant differences in vertical distribution among the sampling dates obtained by the latter method and the χ^2 was very different (Tab. 13). There can, however, be no doubt that the factorial analysis is most correct. Therefore, significant χ^2 obtained in connection with vertical distributions should not be emphasized.

4.3.4.1. *Seasonal variation*

The seasonal variation in vertical distribution could only be examined in area A. Table 13 shows few significant seasonal variations. It appears, however, that some species had a similar seasonal variation in the different sample plots. Therefore, if all sample plots were included in the analysis the seasonal variations in the total number of individuals of all species and in the number of *Cognettia sphagnetorum*, *Enchytronia parva*, and *Enchytraeus norvegicus* were significant (Fig. 18). The variations in the other species were not significant, but as most species included in Fig. 18 exhibited a similar variation, a real variation in the vertical distribution has most probably occurred.

The seasonal variation appeared by a smaller proportion of animals in the 0—4 cm soil layer in July than at the other sampling dates. It is, however, interesting to note that the smaller proportion in July was in general not accompanied by a reduction in the abundance in the same soil layer.

4.3.4.2. *Variation among sample plots*

Statistical analysis of the variation in vertical distribution among the sample plots was also based on the factorial design and could, therefore, only be carried out on the data from area A. The variations among the vegetation types with regard to the vertical distribution of the total enchytraeid population, of *Cognettia sphagnetorum*, *Achaeta* spp., and *Enchytronia parva* were significant at the 0.001 level. The variation among all the sample plots with regard to the abundance in the upper 4 cm of the soil as percentage of the total abundance to 10 cm depth appears from Fig. 19. The figures from area A

Table 12 The index of diversity of the sample plots, its standard deviation, and the 95 % confidence intervall of the contrasts

Study area	Index α Contrast c	Cl-Pn	Ba-Pn	Va-Pn	Eu-Pc My	Eu-Pc Dr	Me-Pc ty	Me-Pc At
A	α	0.39 ± 0.06		0.80 ± 0.11	0.64 ± 0.09		A_1: 1.16 ± 0.12 A_2: 1.11 ± 0.13	2.30 ± 0.23
	c		**0.41 ± 0.26**	0.16 ± 0.28	A_2: **0.47 ± 0.32**			A_1: **1.14 ± 0.52**
B	α		0.24 ± 0.05	0.41 ± 0.14	0.46 ± 0.07	0.47 ± 0.08	0.93 ± 0.12	2.50 ± 0.26
	c		0.17 ± 0.30	0.05 ± 0.31	0.01 ± 0.22	**0.46 ± 0.29**	**1.57 ± 0.58**	
C	α		0.39 ± 0.08	0.49 ± 0.08	0.56 ± 0.08	0.72 ± 0.10	1.40 ± 0.18	2.27 ± 0.21
	c		0.10 ± 0.22	0.07 ± 0.23	0.16 ± 0.25	**0.68 ± 0.41**	**0.87 ± 0.55**	

Table 13 Differences in the significance level of the seasonal variation in the vertical distribution when analysed by χ^2 and factorial analysis (area A)

Vegetation type and species	χ^2 22. V—13. VII	13. VII—3. IX	3. IX—25. X	Factorial analysis
Cl-Pn				
C. sphagnetorum	$P < 0.001$	$P < 0.001$	$P < 0.001$	n. s.
Va-Pn				
C. sphagnetorum	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.0025$
Eu-Pc My				
C. sphagnetorum	n. s.	$P < 0.001$	$P < 0.001$	n. s.
Me-Pc ty A_1				
E. parva	$P < 0.001$	$P < 0.001$	$P < 0.001$	n. s.
Me-Pc ty A_2				
E. parva	$P < 0.05$	$P < 0.01$	$P < 0.001$	n. s.

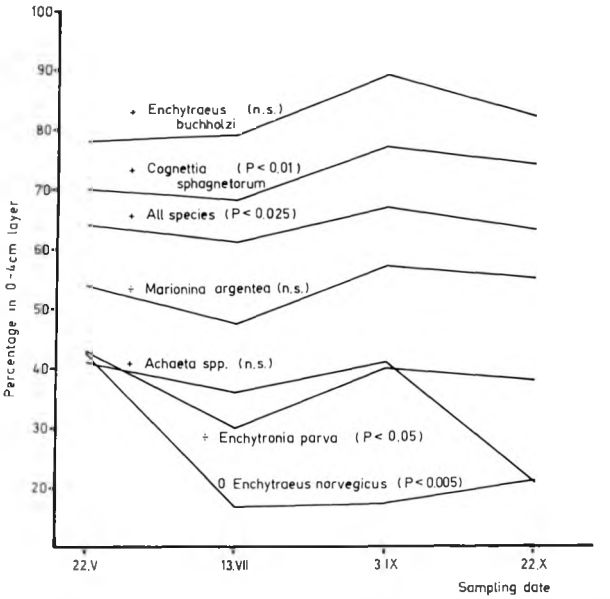

Fig. 18 Seasonal variation in the number of individuals in the upper 4 cm of the soil as percentage of the total number to 10 cm depth (area A). (+) increasing, (÷) decreasing abundance in the 0—4 cm layer from 22. V to 13. VII, (0) no change in abundance.

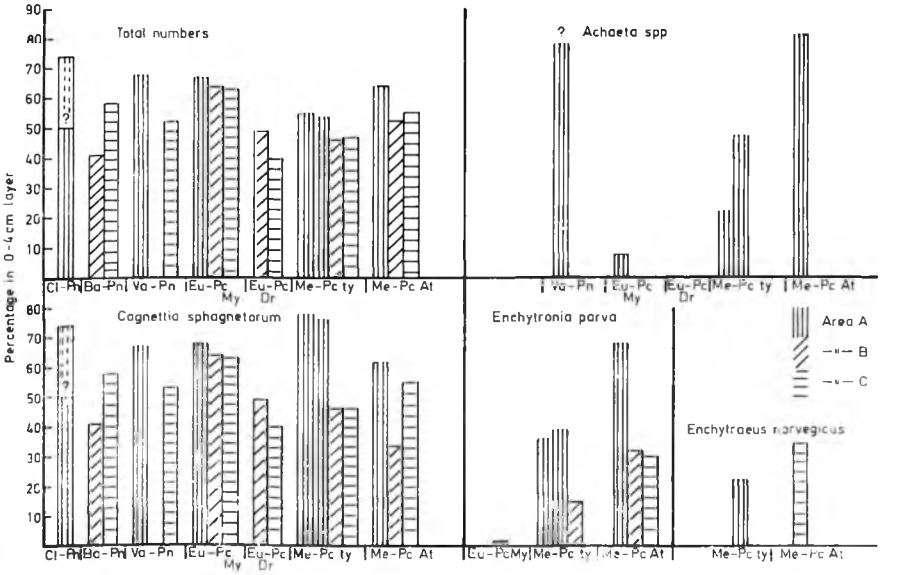

Fig. 19 The number of individuals in the 0—4 cm soil layer at the different vegetation types as percentage of the number of individuals in the entire samples.

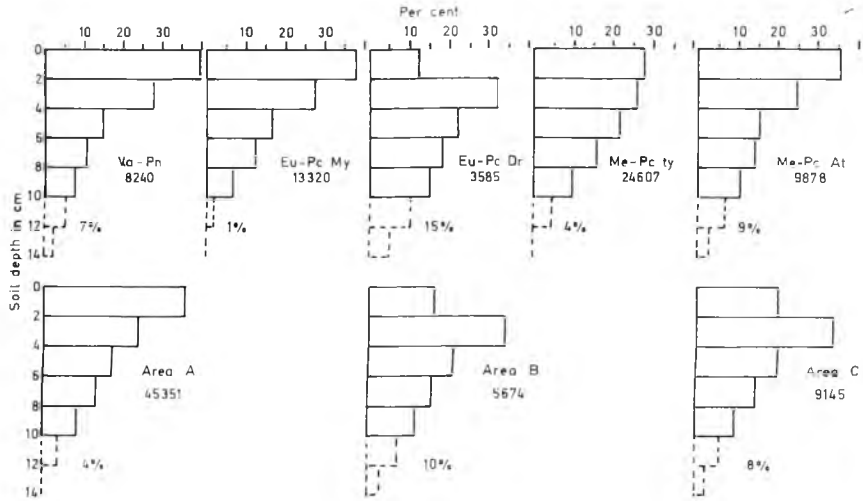

Fig. 20 The average relative abundance of enchytraeids in different soil layers. The abundance below 10 cm is estimated by extrapolation. The **Eu-Pc Dr** originates from area B and C only. Figures beside each histogram give the number of individuals used in the calculation.

represent the averages of the four samples. Due to the variation in stone content and therefore, in the depth of the soil cores (Table 7), the proportions in the figure are based on different number of sample units. This implies that the precision of the estimated proportions is unequal. The **Cl-Pn** (area A) consisted partly of raw humus upon rocks, partly of peat. The vertical distribution in peat was much more even and the abundance was smaller than in raw humus. Therefore, the vertical distribution on this vegetation type varied as indicated in Fig. 19. Exclusion of this vegetation type did not, however, alter the significance of the variation in the vertical distribution in area A.

Fig. 19 reveals that the proportion of animals in the topmost layers of the soil varied both with the vegetation types and the study areas. This implies probably that unequal proportions of the enchytraeid population have been considered in the various sample plots. This appears from Fig. 20 which gives the average vertical distribution of the study areas and most vegetation types. By means of extrapolations rough estimates were obtained of the abundance below 10 cm in per cent of the abundance above 10 cm. It is seen that only ca. 85 % of the population in the **Eu-Pc Dr** and almost 100 % in the **Eu-Pc My** might have been taken into account. It is also seen that the samples in area B and C included a smaller proportion of the population than the sampes in area A.

The proportion of individuals (in 0—5 cm soil delpth) of species common to several vegetationl types increased in general from the **Eu-Pc** to the **Me-Pc Af** (Fig. 19). *Cognettia sphagnetorum* was rather rare at the Athyrium subassociation and the estimated proportion is imprecise. The high proportion of *Achaeta* spp. at the **Va-Pn** is also uncertain as almost all individuals were found in two sample units in July. In the other sample units and at the other sampling dates the species was restricted to the mineral soil.

4.3.4.3. *Variation among species*

In psite of the significant variations in vertical distribution caused by differences in the soil and dates for sampling, there was conspicious differences in the average vertical distribution among several species (Fig. 21).

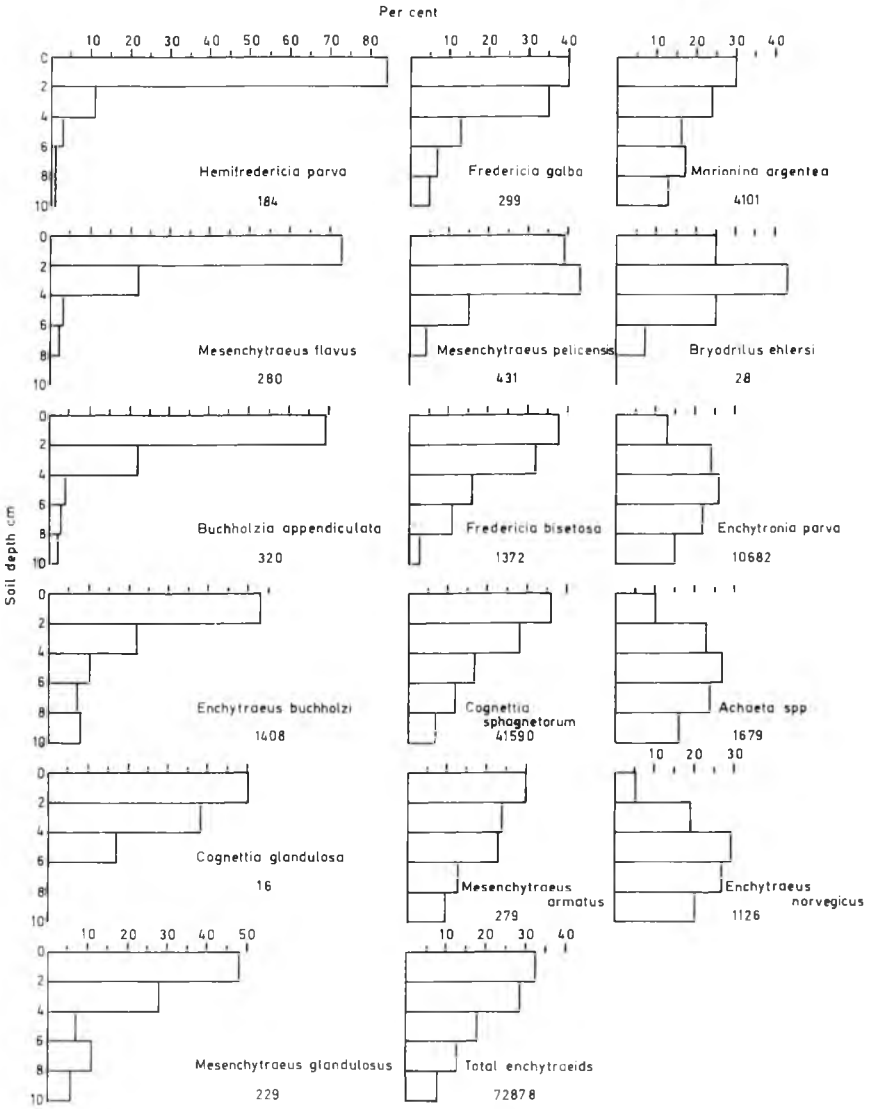

Fig. 21 The average relative abundance of enchytraeids in different soil layers. The total number of individuals of each species is presented.

To indicate the precision of the different distributions the number of individuals of each species is given. It is, however, purposeless to test the differences among species by χ^2. Just to indicate the results of such a method the distribution of two similarily distributed species were compared viz. *Fredericia bisetosa* and *Cognettia sphagnetorum*. The difference between the two species in the vertical distribution was significant at the 0.001 probability level. *Fredericia bisetosa* and *F. paroniana* seemed to have an almost identical vertical distribution. and, therefore, only the former species was included in the figure. Other species that might have been included are *Fredericia bulbosa* and *F. ratzeli*.

However, both species were rare, and the variation among the sample plots was so great that no definite vertical distribution could be established.

4.3.5. *Relation between vegetation, abiotic factors, and enchytraeid fauna*

4.3.5.1. *Vegetation*

The occurrence of the enchytraeid species on the different vegetation types implies that the species may have a distribution similar to various plant species (Table 4 and 9). *Cognettia sphagnetorum* and probably *Mesenchytraeus pelicensis* may be distributed similar to *Vaccinium myrtillus*, *V. vitis-idaea*, *Deshampsia flexuosa*, *Luzula pilosa*, *Pleurozium schreberi*, *Dicranum rugosum*, *D. scoparium*, and *Hylocomium splendens*. Species like *Mesenchytraeus glandulosus*, *M. flavus*, *Achaeta* spp., and *Bryodrilus ehlersi* may be indirectly associated to *Maianthemum biofolium*, *Trientalis europaea*, *Linnaea borealis*, and others. *Enchytronia parva*, *Enchytraeus buchholzi*, and *E. norvegicus* are probably associated with the plant species of the **Me-Pc** association for which *Carex digitata*, *Melampyrum silvaticum*, *Melica nutans*, *Viola riviniana*, and various moss species are most typical. The majority of the enchytraeid species registered in this study was restricted to the **Me-Pc At** and consequently associated with the plant species of this subassociation.

It will also be noticed that the poorest vegetation types had characteristic plant species (Table 4) but no characteristic enchytraeid species (Table 9). Despite this it seems to be a close relationship between the number of plant species and the number of enchytraeid species recorded in this study (Fig. 22).

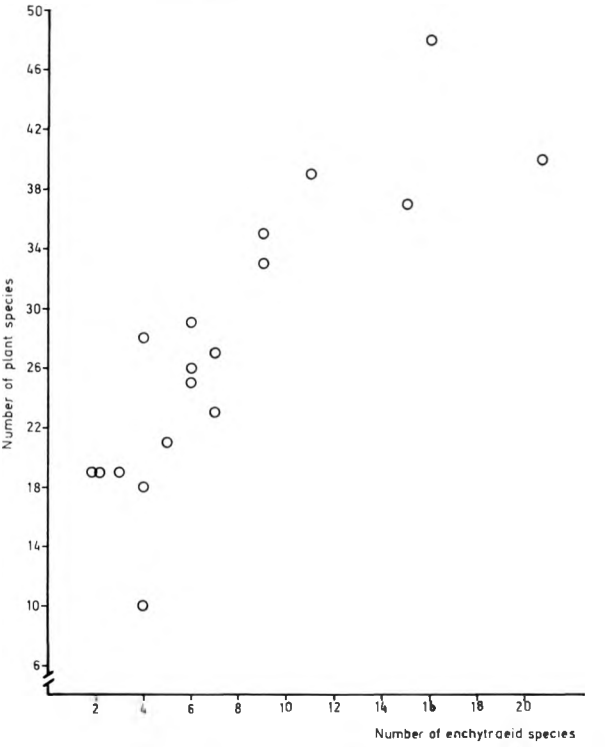

Fig. 22 Relation between the number of plant species and enchytraeid species.

4.3.5.2. *Abiotic factors*

There was a significant relation between the soil profiles and the occurrence of different enchytraeid species. The typical species of **Me-Pc At** were restricted to brown earth and the typical species of the **Me-Pc** association were restricted to brown earth and semipodzol. Some species of the latter group, however, viz. *Achaeta* spp., *Enchytronia parva*, and *Enchytraeus norvegicus* were in contrast to the other species most abundant in 2—8 cm soil depth (Fig. 21). This indicates that the species were associated with mineral soils. Species living in mineral soils are more influenced by the soil texture than other species. It is, therefore, interesting to note that *E. parva* was most abundant in sandy soil where the fractions 0.02—0.6 mm dominated. *E. norvegicus* was similarly most abundant in soils dominated by the fraction 0.6—2 mm (Table 9, Fig. 7). These soils may be characterized as sediments. *Achaeta* spp. on the other hand does not seem to be restricted to sedimentary soils but it seems to prefer sandy soils.

Cognettia sphagnetorum, *Mesenchytraeus pelicensis*, and especially *M. glandulosus* and *M. flavus* may be characterized as epedaphic species (Fig. 21). This implies that they seem to be associated with humus material and their abundance in mineral soil was small. Table 14 shows the densities of *C. sphagnetorum* in raw humus, in the A_2 layer, and in peat. The low abundance in the last mentioned humus type should be noticed.

Table 14 Abundance (per dm³) of *Cognettia sphagnetorum* in different soils

	Cl-Pn	Ba-Pn		Va-Pn			Eu-Pc My			Average
	A	B	C	A	B	C	A	B	C	
Raw humus	851	388	331	380	8	482	439	780	1120	531
Peat	128	68	80	—	—	—	—	—	—	92
Mineral soil A_2 layer	547*)	363*)	75	126	23	399	91	263	215	234

*) A_1 layer

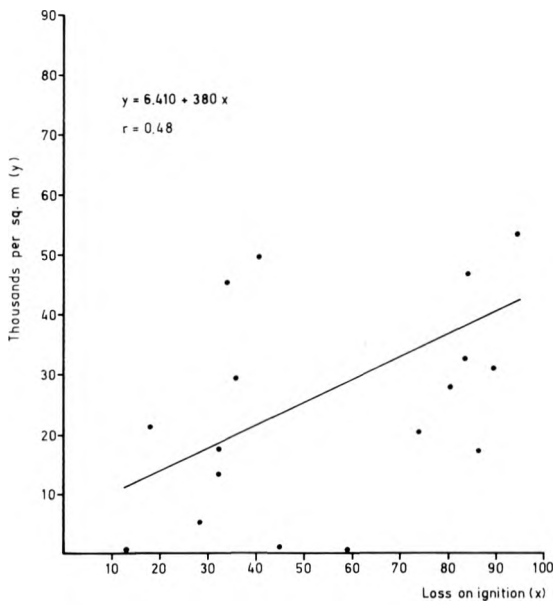

Fig. 23 Relation between the abundance of *Cognettia sphagnetorum* and the loss on ignition.

The relationship between *C. sphagnetorum* and the amount of organic matter may also be seen by comparing the abundance of the species (Table 9) at the various sample plots with the corresponding loss on ignition (Table 8). A regression analysis of this material (Fig. 23) showed that the regression coefficient is significantly different from zero ($t = 2.16$, $df = 16$).

However, relationships between chemical or soil water conditions on the one hand and the densities of some species on the other hand were intended to be studied by means of the three corresponding soil cores as mentioned in Chapter 3.1. This method, however, revealed no conspicuous correlations.

The average soil moisture, however, seemed to influence the mean densities of the sample plots. Comparison of Figs. 10 and 18 shows that the seasonal variation in the relative number of individuals in the upper 4 cm of the soil was similar to the seasonal variation in the soil moisture. Figs. 9 and 19 also reveal that the number of individuals in the upper 4 cm of the soil in the three study areas seemed to be related to the soil moisture. The variation in the soil moisture was, however, greatest in the upper layer of the soil (0—2 cm). Therefore, in Fig. 24 the relative number of individuals of *C. sphagnetorum* in the 0—2 cm layer of the different sample plots was plotted against the corresponding values of the soil moisture. The correlation coefficient was significant at the 0.001 probability level. However, the figure seems to reveal correlation between the abundance and the soil moisture in area B and C, but not in area A. This assumption was supported by regression analysis. Despite the fact that calculations did not indicate any non-linear relationship between the abundance of enchytraeids and soil moisture, it is reasonable that such a relationship in reality exists.

If the observations from area A and the **Me-Pc At** in area B (only 59 specimens were found) were excluded from the regression analysis, the intersection between this new

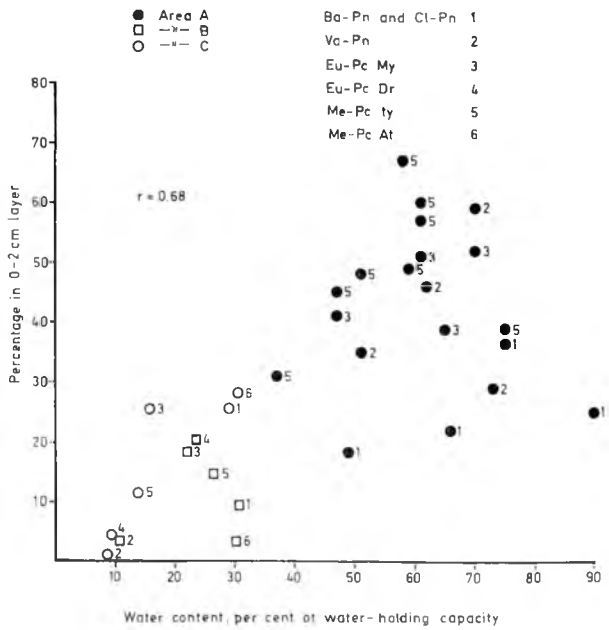

Fig. 24 The relation between the soil moisture and the abundance of *Cognettia sphagnetorum* in the 0—2 cm soil layer as percentage of the abundance in the entire samples.

regression and the x-axis is at ca 3.5% of the water-holding capacity at pF 0.5. This means that the probability is very low that animals can survive when the soil moisture is below this value. However, if assuming the non-linear relationship it is more likely that the "minimal moisture content" was slightly below 10% of the water-holding capacity at pF 0.5.

5. Discussion

5.1. Vegetation

The distribution of the plant species to the vegetation types is in agreement with the records of DAHL et al. (1967). A few species were observed on other vegetation types than those being typical for the species. As, however, no similar variations in the abiotic and faunistic properties of the soil were observed the deviations in the floristic composition are not emphasized.

The similarities among the vegetation types were in general smaller in this study than observed by DAHL et al. (1967). Most of this discrepancy is probably explained by the higher number of species recorded in area A compared with area B and C. The **Me-Pc At** sample plot in area A was the plant community most different from the other vegetation type (Fig. 6). According to KIELLAND-LUND (personal communication) it may be questionable that the sample plot really belongs to the **Me-Pc At**. The vegetation type may have been influenced by human activity.

5.2. Abiotic factors

The relation between vegetation types and soil profiles has previously been examined in Norway by LÅG (e. g. 1959a and b, 1961). These studies have shown that the frequence of brown earth is very small in poorer sites than the **Me-Pc**. This agrees with the observations in the present study.

The relations between soil texture and vegetation types on the other hand, have not been much examined. LÅG (1961) mentions that the amounts of fine particles are greater in brown earth than in podzols and DAHL et al. (1967) tell that the **Va-Pn** is found on sandy plains in the lowlands of Southern Fennoscandia. These observations also agree with the results shown in Fig. 7. It appears that the **Va-Pn** was located on sediments dominated by the coarse and medium sand fractions (2—0.2 mm), and also that the average content of fine particles were much greater at the **Me-Pc At** than ta the other vegetation types.

The chemical properties of the soil within the vegetation types exhibited great variations. Statistical analysis to discriminate among the vegetation types, must, therefore, be based on a larger number of replicates than available in the present study. DAHL et al. (1967), however, found that the content of nitrogen, the base saturation, and the amounts of Mn increased significantly from the **Vu-Pn** to the **Me-Pc At**. The loss on ignition and the amounts of Mg and Na on the other hand, decreased in the same direction. The reported variation in the base saturation, the contents of nitrogen, and the loss on ignition are supported by the present study. These factors were also found by DAHL et al. (1967) to be most important in discriminating among the vegetation types. The variation in these factors among the pine vegetation types and to some extent also between the **Eu-Pc My** and the pine types, however, was small and mostly not significant.

The different variation in the water-holding capacity with increasing soil depth observed especially between the brown earth and the podzol profiles has presumably mainly two reasons. For the first, the distribution of organic matter is more even in brown earth than in podzol. Secondly, the brown earth and to some extent also the semipodzol soils were finer textured than the podzol soils (Fig. 7). This means that the water-holding

capacity in podzol soils decreased very significantly from the raw humus layer to the mineral soil. A consequence of the coarse-textured soil especially at the **Va-Pn** is that capillary connections between the raw humus and the ground water is unreasonable without a high ground water table. This means that these soils are more exposed to drying than the semipodzols and brown earths (compare Figs. 7 and 9).

In the pine forests in area A the highest soil moisture was found in May. In the spruce forests the highest moisture was found in October. By comparing this with the cover of the trees it may be concluded that the moisture differences most probably were caused by the smaller interception of snow in the three layer and consequently more snow at the ground in pine forest than in the denser spruce forest.

5.3. Enchytraeid fauna

5.3.1. *Species composition*

Twenty three species (including *Cernosvitoviella* sp.) have been recorded and only *Achaeta aberrans* and *Hemifredericia parva* have not previously been registered in Norway. The study supports previous conclusions (Nurminen 1967a, Abrahamsen 1968) that *Cognettia sphagnetorum* is the dominating species in Fennoscandian coniferous forest soil. The other typical species of coniferous forests are considerably less abundant and their dominance was always smaller than 10 % and usually smaller than 1 %. Compared with Finnish studies (e. g. Nurminen 1967a) the present study has revealed higher densities of *Mesenchytraeus glandulosus*, *Mesenchytraeus pelicensis*, and *Achaeta* spp. and smaller densities of *Cognettia glandulosa*, *Bryodrilus ehlersi*, and probably *Mesenchytraeus flavus*.

In addition to the species previously recorded from Norwegian nutrituous spruce forest soil (Nurminen 1967b, Abrahamsen 1968) the following species have been found: *Achaeta aberrans*, *Henlea nasuta*, *Hemifredericia parva*, and *Fredericia leydigi*. These species, however, were not very abundant (dominance < 1—8 %). Of the typical species in nutritious spruce forest soil the only species recorded in Finland is *Buchholzia appendiculata*. The low number of exacting species however, may be due to the small number of samples collected in nutritious soils in Finland.

The present study also supports previous conclusion (Abrahamsen 1968) on the difference between the species composition in coniferous forest soil in Fennoscandia and England (O'Connor 1957, Springett 1963).

5.3.2. *Abundance*

5.3.2.1. *Seasonal variation*

Previous studies from the Nordic countries have revealed minimal abundance of enchytraeids which can be related to drought periods in May—June (Nielsen 1955a, Nurminen 1967a). In the present study a contrary trend was noticed. The densities in general (Fig. 13) increased from May to July despite decreasing water content in the soil (Fig. 10). The water content in July was, however, not observed below ca. 35 % of the water-holding capacity at pF 0.5 which may indicate that this value hardly causes significant reduction of the population. This suggestion is supported by Fig. 24 and by a laboratory experiment (Abrahamsen 1971) on the reproduction of *Cognettia sphagnetorum* in relation to temperature and soil moisture. In this study the optimal moisture was found to be between ca. 50 and 95 % of the water-holding capacity at pF 0.5, but severe reduction of the reproduction rate was only observed when the moisture was below ca. 25 %. The possibility of specific variation in the soil moisture requirements should, however, be stressed. The abundance of *Marionina argentea* was for example significantly smaller in July than at the other sampling dates.

The increasing abundance in general from May to July must be explained by the increasing temperature (Fig. 11). The effect of the temperature on the reproduction of enchytraeids is only sparsely investigated. But Reynoldson (1943) observed 18 °C as an approximate optimal breeding temperature for *Enchytraeus albidus* Henle, 1937, and *Lumbricillus lineatus* (O. F. Müller, 1774). The temperature range for reproduction was between 5 and 25 °C. Sauerlandt and Marzusch-Trappmann (1959) mention the optimum breeding temperature for *Enchytraeus buchholzi* to be between 25 and 28 °C. The laboratory experiment on *Cognettia sphagnetorum* (Abrahamsen 1971) showed that after five months the number of individuals at 6° and 12 °C was only ca. 5 and ca. 25 per cent of the number at 18 °C. Therefore, the length of the period in which the temperature is above say 12 °C may be of great importance for the abundance.

The difference in seasonal variation in abundance between the pine and spruce forests is of some interest. As mentioned (Chapter 5.2.) smaller interception of snow in the wintertime probably was the reason for the moister soil in the pine forests in the early summer than in the spruce forests (Fig. 10). Together with increasing temperature (Fig. 11) this may be the reason for the fast growth of the population of *Cognettia sphagnetorum* observed in area A in the early summer (Fig. 13). The pine forests are, however, usually found on coarse textured soils (e. g. Dahl et al. 1967) involving less stable moisture conditions than in spruce forests. Therefore, greater seasonal fluctuations in the abundance of soil animals are to be expected in pine forests than in spruce forests.

5.3.2.2. *Variation in the total abundance and among the sample plots*

Tab. 15 reveals a comparison of the abundance per sq. m of enchytraeids registered in different studies in coniferous forest soil. Due to intra- and interannual fluctuations in the abundance comparisons of this kind may be of little value. However, some conclusions may be drawn from the table: The abundance of enchytraeids seems to increase from Fennoscandia through Denmark to England. This suggestion is supported by shortcut rank tests (e. g. Snedecor and Cochran 1968) which also revealed significantly smaller abundance in Finland than in Norway. It should be emphasized that the mean values from Finland are based on annual means i. e. including the low densities in wintertime, while all Norwegian data have been obtained from May to December. However, if the densities in the period December—April are excluded from the Finnish data the mean abundances increase only slightly.

The differences in abundance may mainly be caused by climatic variations. O'Connor's (1957) study in Wales was carried out in humid area (200 to 225 days with rain per year) where the average mean monthly air temperature ranged from 5.5 to 15.5 °C. In the Danish area the mean monthly temperature ranged from 0 to 22 °C (O'Connor 1967), but the precipitation was considerably smaller, especially in the period April—June in the investigation years (Nielsen 1955a and b). The temperatures in the sample areas in Fennoscandia seem to be similar (Fig. 10 and Huhta et al. 1967) and the snow is usually lying from December to April. The precipitation on the other hand is considerably smaller in the Finnish areas (ca. 630 mm per year) and the summer drought seems to be much more pronounced than in the Norwegian areas.

The climatological considerations make it reasonable that the highest population densities are registered in England. In Denmark where the temperature also is favourable the populations may be severely diminished once a year due to drought. However, the period with temperatures above e. g. 12 °C is probably approximately 2 months longer in Denmark than in the areas of interest in Fennoscandia. This means that the growth period for the population after the summer drought is longer than in Finland. In Fennoscandia the populations also are reduced in the winter (Nurminen 1967a), and the winter

minima seem to be much deeper than registered in England (e. g. O'Connor 1967). The differences in abundance between Finland and Norway may be explained by the lower frequency of summer drought within the sample areas in Norway.

The most abundant enchytraeid populations were found at the **Eu-Pe**, the **Me-Pe ty** and the **Cl-Pn**. **Cl-Pn** in general, has probably not the most abundant populations due to shallow soil layer (or coarsetextured mineral soil) which must be easily exposed to drought. Enchytraeid and other soil animal populations seem on the whole to be more dependant on an evenly distributed precipitation in natural pine forests than in natural spruce forests. Due to the drought periods occurring almost every summer it is therefore, likely that the abundance of these animals in general is smaller in pine forests than in spruce forests. Table 15 supports this conclusion.

Table 15 The abundance of Enchytraeidae in coniferous forest soil registered in various studies

Reference Country	Habitat	Sample depth cm	Nos. per sq. m in thousands min.	mean	max.
Nielsen, 1955a Denmark	Spruce plantations	5	9.4	45.1	101.0
	Pine plantations	5	29.2	61.4	108.0
O'Connor, 1957 England	Douglas-fir plantation	6	42.0	143.3[1])	250.0
Springett, 1963 England	Pine plantations	6		81.3	
Nurminen, 1967a Finland	Spruce loc. 1	ca. 5	1.8	16.2	53.6
	Pine loc. 7	ca. 5	0.4	10.7	36.8
Abrahamsen, 1969a Norway	Spruce	6[2])	7.6	43.0	85.5
Abrahamsen, 1970 Norway	Pine	ca. 5	3.2	34.7	54.7
The present paper	Spruce	6	12.7	34.7	73.9
	Pine	6	0.8	22.9	47.8

1) Mean number obtained from O'Connor (1963).
2) Original soil depth 2 and 3 cm. Figures corrected according to the vertical distribution.

In a Finnish study (Huhta et al. 1967) higher abundances of most soil animals (including enchytraeids) were also found in spruce forests (MT and OMT) than in pine forests (CT and VT). According to Cajander (1962) the MT and OMT belong to "the moist moss-forest class" and the CT and VT belong to "the dry moss- (and lichen-) forest class". Therefore, as the CT and VT correspond approximately to the **Cl-Pn** and **Va-Pn** respectively, and the MT and OMT correspond to the two **Eu-Pe** subassociations the results of the two studies support each other.

It should be emphasized that the water content is only one among many factors regulating the population density of soil animals in coniferous forest. In addition to the **Va-Pn**, the **Ba-Pn** and **Me-Pe At** had the lowest densities of enchytraeids despite the fact that the two last mentioned types were the moistest ones.

The abundance of the various species can only to some extent be compared with other papers. Nurminen (1967a) found that 98—100 % of the enchytraeid population in coniferous forests consisted of *Cognettia sphagnetorum* (see Table 15). Springett (1963) recorded ca. 35.000 specimens of *C. sphagnetorum* per sq. m (42 per cent of the total abundance) in pine forests and 114.000 in Nardus grassland. The latter number is probably the highest density recorded of this species. In two previous studies (Abra-

HAMSEN 1969a and 1970) the abundance of *C. sphagnetorum* in coniferous forests varied from 1.500 to 47.000 per sq. m, and in the present study the highest density was 84.000. In a "dry Calluna type on sugar limestone" SPRINGETT (1968) recorded 96.000 specimens of *C. sphagnetorum* which was the highest number recorded from the ecosystems examined.

The other typical species in coniferous forest soil never seem to be very abundant. The highest density observed of *Mesenchytraeus glandulosus* seems to be 1.700 per sq. m in a pine forest in England (SPRINGETT 1963). In the present study the highest density was 1.000 at the **Me-Pc ty**, area C. *Mesenchytraeus pelicensis* seems to be a very rare species outside Norway. In a previous study ca. 2.000 individuals per sq. m have been recorded (ABRAHAMSEN 1969a) but in an urea fertilization experiment more than 3.000 individuals per sq. m were registered (ABRAHAMSEN 1970). The highest density of *Mesenchytraeus flavus* registered in Norway is 750 per sq. m at the **Me-Pc ty** A_1. At this vegetation type the species may have its greatest abundance. In the fertilization experiment application of urea resulted in increased breeding and 600 specimens were noticed per sq. m. NURMINEN (1967a) has found this species to constitute up to 10—15 % of the total enchytraeid population. This corresponds probably to ca. 3.500 individuals per sq. m which is similar to the density registered by PEACHEY (1963) in Nardus grassland. *Bryodrilus ehlersi* has only been observed sporadically in this study but on MT in spruce and pine forest in Finland almost 20.000 individuals per sq. m may have been observed (HUHTA et al. 1967, NURMINEN 1967a). All species mentioned hitherto seem to be most abundant in coniferous forest soil or in Nardus grassland which according to the distribution of *Nardus stricta* in Norway may have many similarities.

Enchytronia parva seems to reach its greatest abundance in nutritious spruce forest soil. In this study the maximal abundance recorded is almost 25.000 per sq. m and in a previous study the highest density was 18.500 (ABRAHAMSEN 1969a). The species has also been recorded in deciduous forest and in meadows but no comments were made on the abundance (NIELSEN and CHRISTENSEN 1959, ABRAHAMSEN 1968). The other species recorded in Norwegian coniferous forest inhabited nutritious soil and they are probably more abundant in other ecosystems. SPRINGETT (1968) recorded 6.000 individuals per sq. m of *Enchytraeus buchholzi* in a Festuca grassland and in a moist stream edge. This number was slightly higher than registered in the present study (Table 9, Fig. 13). *Fredericia bisetosa* seems to be especially abundant in pasture soil in Denmark where NIELSEN (1954) probably recorded almost 50.000 specimens per sq. m which is more than twice as much as registered in this study (Tab. 9). The highest number of *Fredericia galba* registered in the present study (1.400 per sq. m) is slightly smaller than the densities observed by SPRINGETT (1968) in a Kobresia site (1.000—1.900 per sq. m) and Festuca grassland (1.300—1.500 per sq. m). SPRINGETT (1968) registered ca. 21.000 *Marionina argentea* in a moist Kobresia site and this number is slightly higher than the maximal density observed in the present study (ca. 19.000). SPRINGETT (1968) also registered higher densities of *Buchholzia appendiculata* (5.800 in Festuca grassland) than registered in the present study. *Mesenchytraeus armatus* on the other hand may be more common in nutritious spruce forest (3.600 at the **Me-Pc At** area B) than in any of the sites examined by SPRINGETT (1968).

5.3.3. *Relation between number of species and number of individuals*

The index of diversity (FISHER et al. 1943) is independent of the sample size. Fig. 15, however, indicates that α increases with increasing number of individuals. Similar relations have been reported by FISHER et al. (1943), and WILLIAMS (1953), and it was explained by seasonal variations in the diversity or by variations caused by the sampling. Seasonal variations in the diversity have later been demonstrated, e. g. by LEWIS (1969).

If, however, the sample units in the four samples from the different sample plots were considered as one large sample and the cumulative sum of species and individuals were obtained by adding the 80 sample units in a random way, the seasonal variation in α might be removed. The figures obtained in this way, however, were almost identical to those reported in Fig. 15. This indicates as Fig. 16, that the logarithmic series do not fit the enchytraeid counts. Wood (1967a) reached the same conclusion with regard to soil microarthropods. He also noticed a sigmoid relationship between the number of species and individuals. This is typical for the log-normal distribution. According to Williams (1953) the sigmoid nature of the curve will not appear graphically until the sample contains 80—90 % of the species in the population. Estimates of the total number of species in the populations indicate that ca. 90 % of the species in the **Me-Pc** were found. No obvious sigmoid relationship could be found in the data from the Athyrium subassociation, but the sigmoid nature may be indicated in the data of typical subassociation.

The "minimal area" has many definitions (e. g. Goodall 1952, Dahl 1956, Greig-Smith 1964). Haarløv (1960) was probably one of the first to apply the "minimal area" in zoological connections. He used Goodall's definition "an area below which the association cannot develop all its characteristic features...", and suggested that if species with frequencies above 60 % were included in the area, "the characteristic features" were at hand. For microarthropods in pasture soil this definition resulted in a minimal area of 5 to 10 sq. cm. Haarløv, however, stressed that this result was of importance for practical field work where the intention was to collect typical species. No comments were made relating to the minimal area giving a certain fraction of the species. On the other hand Wood (1967a) has given species-individuals curves for soil microarthropods in different moorland soils. These curves were based on very large number of individuals, and very high proportions of the species in the populations were most probably recorded. On the basis of Wood's data it is possible to suggest that to obtain, e. g. ca. 80 % of the microarthropod species in these habitats, it would be necessary to collect 3.000—7.000 individuals dependent on the homogenity of the populations. These numbers are considerably higher than those reported in the present study (200—4.500). The higher number of individuals is however, likely as the number of microarthropod species is much greater than the number of enchytraeid species. This means that the number of rare species in particular, is very large.

The variation among the vegetation types and also among the study areas with regard to the index of diversity support the conclusion that the main differences among the vegetation types are found in the spruce forests.

5.3.4. *Vertical distribution*

5.3.4.1. *Seasonal variation*

Seasonal variation in the vertical distribution may be caused by vertical migration, or differences in the breeding-or mortality-rates in the different soil layers. Nielsen (1955a and b) observed a tendency of the aminals to move away from the surface layer in drought periods. This tendency was small, but according to Nielsen (1955b) this was due to inconspicuous moisture gradients in the soil. O'Connor (1957) also observed significant reductions of worms in the litter layer in a drought experiment, but as significant reductions of worms in deeper soil layers also were found, he concluded that the variation in vertical distribution rather was due to different mortality rates than to vertical migration. The moisture gradients were small in O'Connor's study too. However, within a few hours Springett et al. (1970) found variations in the vertical distribution correlated with soil moisture. Therefore, it is reasonable to conclude that vertical migration of enchytraeids can be caused by variation in soil moisture.

Temperature may also be an important factor in this respect. PEACHEY (1963) observed significant positive correlations between the relative abundance of enchytraeids in the 0—2 cm soil layer and the soil temperature when varying from below 5 °C to above 10 °C. A similar relation was also found by NURMINEN (1967a) who observed conspicuous variations in the vertical distribution when the temperature varied a few degrees around 0 °C. This variation concerned the relative as well as the absolute numbers. NURMINEN gives an example indicating that at this low temperature the abundance in the mineral soil may multiply several times within a period of one month. A breeding rate like this is very unlikely according to the results of Chapter 3.4., and also according to the breeding rate of *Cognettia sphagnetorum* at 6 °C observed in a laboratory experiment (ABRAHAMSEN 1971). This supports the conclusion of NURMINEN that vertical migration must have occurred.

In the present study too some temperature measurements were carried out in area B and C. The variations in temperature were from 11 to 20 °C in one cm soil depth and from 8 to 14 °C in 9 cm depth. However, no significant correlation was found either with the horizontal or with the vertical distribution. This indicates that variations in the vertical distribution of enchytraeids may be caused by variations in temperature when being below, say 10 °C. It should, however, be stressed that soil moisture and soil temperature influence each other, and they should therefore, be considered together (NIELSEN 1955b).

5.3.4.2. *Variation among the sample plots*

There was conspicious variation in the vertical distribution among the study areas (Fig. 20) which may be attributed to differences in the soil moisture (Chapter 5.4.5.). Apart from this variation, however, the concentration of enchytraeids in the surface layer was most conspicuous in the **Va-Pn**, **Eu-Pc My**, and in the **Me-Pc At** (Figs. 19 and 20). This means that the difference between podzol and brown earth with regard to the vertical distribution of all enchytraeids was rather inconspicuous. At the semipodzols of the **Me-Pc ty** the animals were more evenly distributed in the soil profile, but this was exclusively due to the abundant occurrence of euedaphic species like *Enchytronia parva*, *Enchytraeus norvegicus*, and *Achaeta* spp. (Fig. 21). The abundance of these species was, in general, smaller at the Athyrium subassociation where also more epedaphic species (*Hemifredericia parva*, *Enchytraeus buchholzi*, and *Fredericia bisetosa*) were abundant. The differences between the two **Me-Pc** subassociations with regard to the vertical distribution are, therefore, partly explained by the differences in species composition. However, as previously mentioned some of the species common to the **Me-Pc** subassociations seem to be more epedaphic in the Athyrium subassociation than in the typical subassociation.

These results are mostly not in agreement with previous observations on the vertical distribution of soil animals in podzol and brown earth. MURPHY (1953 and 1955) takes examples from natural and cultivated heathland which show that the former soil has a more epedaphic soil fauna than the latter one. He suggested on this basis that "mull" has a more even vertical distribution than natural heathland. This conclusion is supported by a study in grasslands by WOOD (1967b). He showed that ca. 90 % of the Acari and Collembola populations were found in the upper 4 cm of podzolic brown earth while the corresponding proportion in brown earth was ca. 77 %. The same tendency was also found by SPRINGETT (1963) for enchytraeids. In the upper 3 cm of "Pinus mor soil", "Fagus mull soil", and "Nardus stricta grassland" she observed 88 %, 84 %, and 70 % respectively. However, the small difference between "Pinus mor soil" and "Fagus mull soil" should be noticed. FORSSLUND (1944) on the other hand found variations in the vertical distribution of microarthropods which were similar to those reported in the present study. Table 16 gives a summary of FORSSLUND's figures. The figures of the

table are based on the density per unit volume. The Dryopteris type may be similar to the **Eu-Pc Dr** or **Me-Pc ty**, and the podzolisation may be less than in the Vaccinium type. It is, therefore, also interesting to notice the more even distribution in the Dryopteris type than in both the Vaccinium- and the Geranium type. This is quite in agreement with the results of the present paper.

The even vertical distribution in peat registered in the present study is to some extent supported by the results of SPRINGETT et al. (1970).

Table 16 Vertical distribution of microarthropods in Swedish coniferous forest soil (after FORSSLUND 1943)

Vegetation type Soil profile	Vaccinium Podzol	Dryopteris Podzol	Germanium Brown earth
% in F layer	52—78	58	73
% in H layer	22—48	42	27

There is at the present time no definite explanation on the differences in vertica distribution among the soil types. HAARLØV (1955, 1960), however, found that the pore space in the soil decreases with increasing soil depth. He also observed that the fauna in deeper soil layers consisted only of small species. These observations may have some relevance to the present study. The euedaphic enchytraeid species are small and they were mostly recorded in the nutritious soils of the **Me-Pc** association. Due to the differences in the soil texture and the distribution of organic matter in two **Me-Pc** subassociations it seems reasonable that the pore space is smaller and decreases faster with increasing soil depth (to 10 cm) in the brown earth (**Me-Pc ty**) than in semipodzol (**Me-Pc ty**). In this case it is to be expected that the species would live nearer the soil surface in the brown earth than in the semipodzol.

It should, however, be emphasized that also other factors may cause differences in the vertical distribution among the vegetation types. The distribution of organic matter may influence also because this material seems attractive at least for *Cognettia sphagnetorum* (Fig. 23). Another factor which, however, may be more significant is the differences in soil moisture. The **Me-Pc ty** for example is a dry type having a southern distribution and, in valleys, a southern exposure (KIELLAND-LUND 1967a, DAHL et al. 1967). This vegetation type is, therefore, as the **Va-Pn**, usually drier than the other vegetation types and specially drier than the **Me-Pc At** which often is influenced by seeping water (DAHL et al. 1967). The **Me-Pc ty** may, therefore, have a fauna adapted to dry conditions and in this respect the high densities of *Achaeta* spp., *Enchytronia parva*, and *Enchytraeus norvegicus* should be noted. At the **Me-Pc ty** these species may be forced into more superficial soil layer due to periodical water logging in deeper soil layers.

A consequence of the varying vertical distribution is as WOOD (1967b) has pointed out, that different sample depth should have been used in order to obtain similar proportions of the populations. In this study, however, stones reduced the sample depth and deeper soil cores in area B and C could not be obtained by means of a soil corer.

5.3.4.3. *Variation among species*

The vertical distribution of the total enchytraeid population (Fig. 20) shows that ca. 80 % of the population down to 10 cm soil depth was concentrated in the upper 6 cm of the soil. If the distribution is extrapolated to deeper soil layer, it is seen that the 0—10 cm soil layer probably contained ca. 93 % of the total enchytraeid population. This means that ca. 75 % of the total population was in the 0—6 cm layer. NIELSEN

(1955a) registered 81 % in the upper 5 cm of the soil, but this proportion was based on samples from humid habitats where no significant seasonal variation occurred. However, if only the samples from the most humid periods in area A are included the proportion of animals in the upper 6 cm increases less than 2 %. Also compared with other studies on the vertical distribution of enchytraeids the present results reveal more even vertical distribution of the total number of enchytraeids (O'Connor 1957, Peachey 1963, Springett 1963, Nurminen 1967a, Springett et al. 1970).

Since both soil temperature and soil moisture varied in these studies comparisons of this kind may be of little value. However, still more important variations in the average vertical distribution may be caused by different species composition. In Nielsen's (1955a) study for example the dominating species was *Fredericia bisetosa* which according to Fig. 21 had a more epedaphic distribution than the total enchytraeid population and the dominating species of the present study. The proportion of the *Fredericia bisetosa* population in the upper 6 cm of the soil was ca. 85 % which correspond very well to Nielsen's (1955a) data. The species composition in Nurminen's (1967a) study was very similar to the present one, but he did not give the average vertical distribution due to the great seasonal variation. Therefore, the discrepancy between these two studies should not be empasized.

If considering the vertical distribution of the specific species it is seen that both large and small species lived in the surface layer. The typical euedaphic species (*Enchytronia parva*, *Achaeta* spp., and *Enchytraeus norvegicus*) are small animals. The distribution of the different species shows, however, that most species can live in different soil layers. This implies as Haarløv (1960) has pointed out, that the classification of soil animals into epedaphon, hemiedaphon, and eudaphon is only appropriate for rough generalizations.

5.3.5. *Relation between vegetation, abiotic factors, and enchytraeid fauna*

The distribution of plant- and enchytraeid species is probably related to the same factors. However, these factors of which chemical and physical properties of the soil, climate, existent vegetation, and the composition of soil organisms may be most important, may be of different importance for plant and animal species. Any direct relationship between plant species and enchytraeid species is, therefore, not to be expected (e. g. Nielsen 1955). This means that communities based on the composition of plant- and enchytraeid species most likely will be different (Figs. 6 and 12). Comparisons of this kind, however, should be based on larger number of animal species which means that also other groups of animals should be included.

The most conspicuous differences between the two community systems obtained are found in the grouping of the poorest sites — the pine forests and the oligotrophe spruce forests. The number of enchytraeid species at these sites was very small and the animal communities are probably not very different. The differences seem to be more prominent among the nutritious spruce forests. The plant communities in the pine forests are on the other hand easily separated (Fig. 6 and Dahl et al. 1967). This is interesting as Dahl et al. (1967) found, with regard to chemical properties of the soil, small differences among the pine types and significant differences among the nutritious spruce forest types. This indicates that the species composition of enchytraeids may be as useful in describing the soil conditions as is the ground cover vegetation. If, for example, the same plots were grouped into six communities based on the results of Fig. 12, the average within community-variation in the loss on ignition, and amounts of Ca, Mg, Mn, Na and K seemed to be reduced compared with the variation in Table 8. This result should, however, not be stressed, as no direct relationship between chemical properties of the soil and the

enchytraeid fauna was found by means of the analysis of the individual sample units. But no relation was either found with the soil moisture despite the correlation between the average abundance of *Cognettia sphagnetorum* and average content of soil water (Fig. 24). This shows that the method of taking adjacent soil cores has failed. The reason may be that the moisture and chemical properties of soil vary so much within small areas that the conditions within three adjacent soil cores of the size used are far from identical. This, however, cannot be known without further studies with smaller sample units or preferably by using the same soil cores for animal extraction as for chemical or moisture measurements.

It is difficult to understand that no relation exists between the soil fauna and chemical conditions in the soil. Dunger (1964) concluded that many studies on this problem have been carried out without revealing any direct relations. In this study, however, a slight, but significant positive correlation was found between the loss on ignition and the abundance of *Cognettia sphagnetorum*. Similar relations with soil microarthropods have been indicated by Davis (1963).

The abundance of earthworms was found to be positively correlated to *p*H and the amount of exchangeable Ca (Satchell 1955), and estimates of the yield of inorganic nitrogen components by an earthworm population showed that about 100 kg per ha may be produced per year (Satchell 1967). Furthermore in a laboratory experiment (Abrahamsen in prep.) the mineralization of nitrogen in raw humus material was found to be ca. 15 % greater in humus with enchytraeids than without. All this indicates that relations must exist between parts of the soil fauna and the chemical properties of the soil. These relations are, however, probably associated with other factors and complicated interactions may exist. To solve these problems larger materials are necessary. This implies that further studies on the soil fauna should to greater extent include measurements of chemical properties of the soil.

It has already been pointed out (Chapter 5.3.2.1.) that soil moisture becomes especially restricting when dropping below ca. 25 % of the water-holding capacity at pF 0.5. Somewhere slightly below 10 % is the limit below which no worms can live. The last-mentioned value may correspond to pF ca. 4 (Nielsen 1955b, Abrahamsen 1971). These considerations make it reasonable that the soil moisture has not been a restricting factor for most species in area A. However, the parallel seasonal variation in the soil moisture (Fig. 10) and in the relative abundance in the upper 4 cm of the soil (Fig. 18) indicates that the preferred moisture is above ca. 40 % of the water-holding capacity. Some species may also have a higher optimal moisture than others. *Marionina argentea* was for example significantly less abundant in July (area A) when the soil moisture was slightly smaller than 60 % of the water-holding capacity at pF 0.5 than at the other sampling dates. This species was also less abundant in area B and C where the soil was much drier than in area A. *M. argentae* has previously been recorded from damp localities (Nielsen and Christensen 1959, Abrahamsen 1968), and from seashores and damp arctic areas (Nurminen 1967b).

Mesenchytraeus pelicensis is another species apparently sensitive to drought. In a fertilization experiment (Abrahamsen 1970) its abundance at the control plots decreased from ca. 2.000 per sq. m in 1965 to less than 100 in 1969. In the same period the average monthly precipitation in May—August decreased from ca. 100 to ca. 65 mm. Sensitivity to drought may be one reason why the species is so rare in Finnish coniferous forest soil.

When the relation between soil moisture and abundance of soil animals are to be examined, the moisture should be measured so often that all significant fluctuations in the moisture are discovered. Single measurements cannot give very high correlations between the moisture and population density. It is for example, obvious when considering Fig. 11, that the soil moisture in area B was increased by rainy weather in a period just

before the sampling took place. This increase cannot, however, have influenced the population density to a significant extent. Therefore, in dry periods the population density will in general be smaller than expected according to the soil moisture.

6. Summary

The ground cover vegetation in Norwegian coniferous forest is divided into eight common vegetation types. In three different areas in Southern Norway six of these vegetation types were analysed with regard to vegetation, physical and chemical properties of the soil, and abundance and species composition of Enchytraeidae.

Twenty three enchytraeid species were recorded in this study of which two species have not previously been observed in Norway. The number of species increased from poor to rich soils but conspicuous differences in species composition were only found among the three most productive vegetation types. The soil of these vegetation types was also most different with regard to chemical properties. The species composition of Enchytraeidae may, therefore, give a reliable impression of the soil properties.

By means of SØRENSEN's quotient of similarity the sample plots were classified into units based on both plant species and enchytraeid species. In general the classification of plant species supported the vegetation system used. The classification of enchytraeid species, however, resulted in units different from the vegetation types. The differences were most conspicious among the poorest soil types.

The most abundant enchytraeid populations were found at the Eu-Piceetum and Cladonio-Pinetum associations on iron podzolic soils. The typical Melico-Piceetum subassociation on semipodzolic soils were also inhabited by large populations of enchytraeids.

Significant seasonal variations were observed both in the abundance and vertical distribution of enchytraeids. These variations were most probably caused by variations in soil moisture.

The depth distribution in the total number of enchytraeids varied significantly among the vegetation types. The variation was partly explained by differences in species composition. The Melico-Piceetum subassociation which comprised most euedaphic species had the most even vertical distribution. However, differences in the vertical distribution among the vegetation types were also observed for the specific species. These differences may be explained by differences in soil properties like moisture, texture and thereby pore space.

Soil moisture slightly below 10% of the water-holding capacity at pF 0.5 corresponding to a volumetric water content of ca. 13%, seem to be mortal for the enchytraeids. Also moistures below ca. 25% of the water-holding capacity at pF 0.5 may severely reduce the populations.

Conspicuous relationships among chemical properties of the soil and the abundance of some species have not been found. The methods have, however, probably been inadequate to the purpose.

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Address of the author: Gunnar Abrahamsen, Norwegian Forest Research Institute, P. O. Box 62, N–1432 Ås NLH (Norway).